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The Effect of a Constant Stimulus  
Upon Touch Localization

By Louis Aryah Lurie, A. B.

Assistant in Psychology



Series II.

Vol. IV.

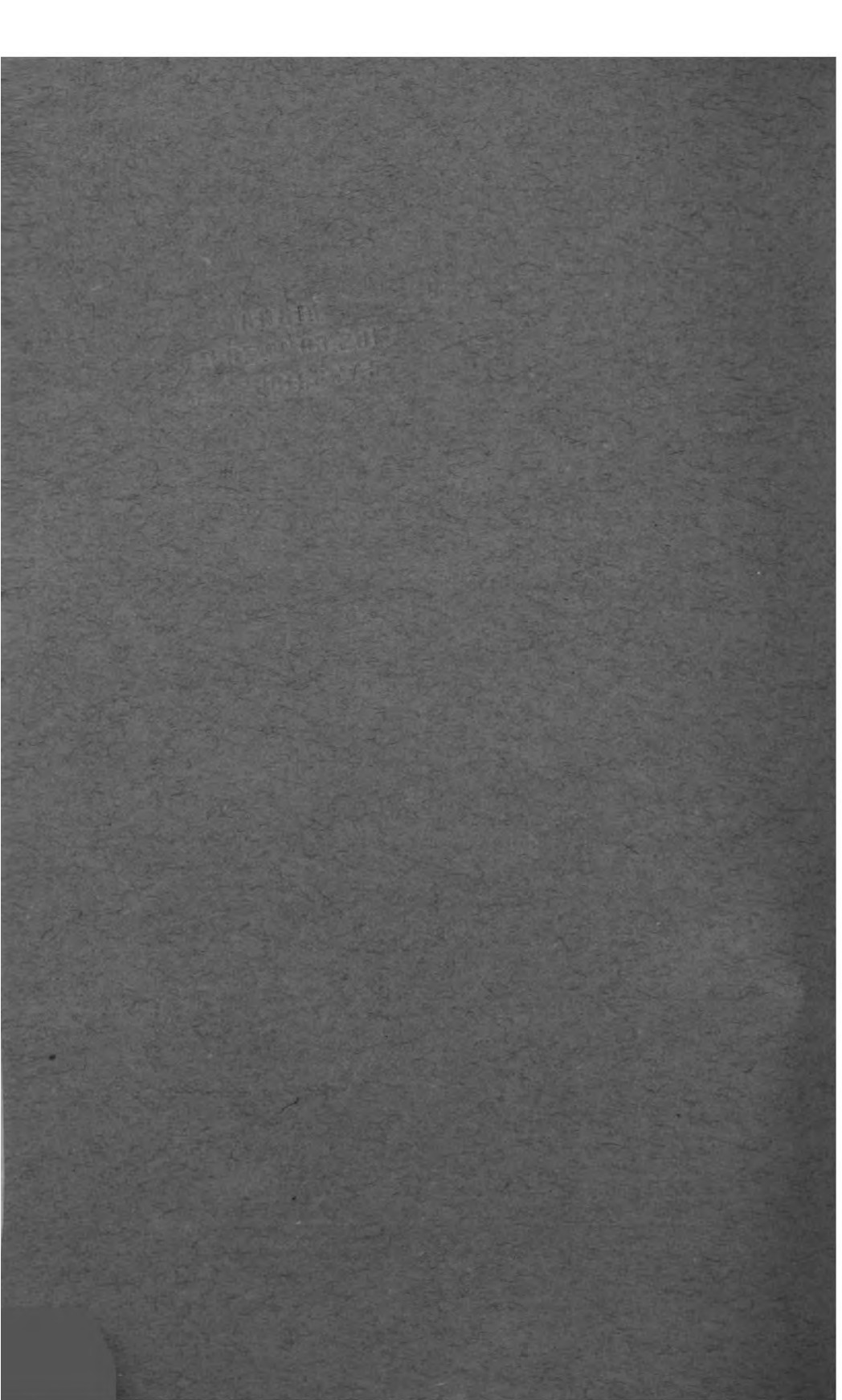
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BY

Louis Aryah Lurie, A. B.

Assistant in Psychology, University of Cincinnati



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## INTRODUCTION

This article is the report of a series of experiments made with the purpose of finding out whether a constant stimulus would influence, in any way, the normal touch localization power of a subject. That is, would the subject's ability of touch localization be increased or diminished; would the direction of the error be drawn toward or away from the point where the constant stimulus was applied; or, on the other hand, would the presence of a constant disturbing element have no effect either on the amount or on the direction of the error? In other words, if a constant stimulus were applied, for example, to the right of a given area, of which the subject's ability of touch localization had been previously determined, would the subject's accuracy be increased or decreased; would the direction of the error be toward the right or toward the left, that is, away from the stimulus, or would the stimulus have no effect whatsoever? It seems reasonable to suppose that a stimulus or sensation, even though in the periphery of the field of attention, if we may so call it, would exert some influence on a subject's discriminative ability; and, based upon this belief, this work was undertaken.

In connection with this problem, another point was considered. If two corresponding points, on both hands, were stimulated simultaneously, what would be the effect on the subject's localization ability? Would his discriminative ability be increased, or would the simultaneous stimulation of corresponding points be similar in its influence to that of the constant stimulus? In other words, would the subject, when asked to locate the spot touched on the practiced hand, after being touched simultaneously upon corresponding points, be more accurate?

My sincere thanks are due to Professor B. B. Breese, at whose suggestion this work was undertaken, and for whose encouragement and valuable assistance I am greatly indebted.

LOUIS ABRAHAM LURIE.

University of Cincinnati.



## METHOD

The subject was a student who, although not thoroughly acquainted with psychological methods and analyses, was still one whose introspection and accuracy of statement could be relied upon. The method of procedure was as follows: First, an area, 30 millimeters square, was marked off on the back of the subject's left hand. The square was outlined by dots placed five millimeters apart. Since the experimentation was divided into a number of sittings, it was essential that the same area should be delimited every time. And since it was evident that the subject could not go around for several months with the back of his hand tattooed with red dots in the form of a 30 millimeter square, some scheme had to be devised by which the experimenter could be fairly certain that the same area would always be marked off. Therefore, an outline of the subject's hand was made and the square drawn in, its relative position being obtained from certain prominent anatomical landmarks, such as the knuckles, the rounded prominence formed by the head of the ulna, the extensor tendons, and the superficial veins (Fig. 1). Consequently, whenever it was necessary to draw the square, the experimenter had only to refer to the diagram with its guiding points to obtain its exact position on the subject's hand. On this diagram were also marked the places where the constant stimuli were applied, thus insuring the stimulation of the same area every time.

The normal stimulus was applied with a pressure-point similar to the one pictured in Titchener's *Experimental Psychology*. The constant stimulus was applied by means of a clamp, which in turn, by means of a screw, could be loosened or tightened, thereby insuring an equal amount of stimulation in every case. The clamp was tightened until the sensation was just short of being very painful. The intensity of the sensation was equal to 5 as measured on Cattell's algometer. During all the experiments, while the normal stimulus was applied, the subject kept his eyes closed, but was permitted to open them when locating the spot which had been touched.

The subject's normal ability of localization was first determined; then the constant stimulus was applied (a) to the tip of the middle finger, (b) to the right of the square, and

(c) to the left of the square. Between experiments *b* and *c* a number of tests was made without the presence of the constant stimulus, in order to see whether or not the subject still retained his normal discriminative power.

The experiments were made during the months of February, March, and April.

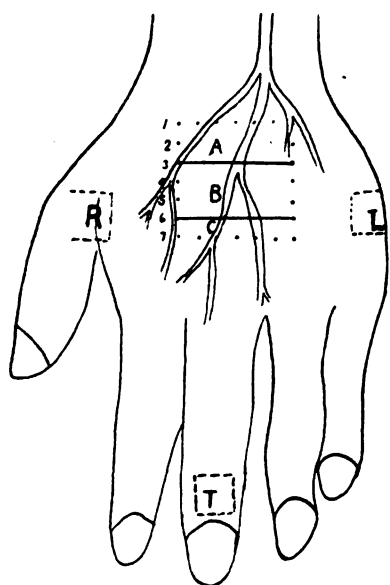


Fig. 1

## Part I:

### CONSIDERATIONS OF THE VARIABILITY OF ERRORS.

#### Experiment No. 1.

The subject closed his eyes and the pressure-point was applied lightly; whereupon he opened his eyes and placed a pencil point on the spot which he supposed had been stimulated. This operation was repeated for about seven hundred times, note being made of both the amount and the direction of the error. The experimenter followed no regular order in touching the hand, but jumped promiscuously from one part of the square to another. Tables I and II give the results:

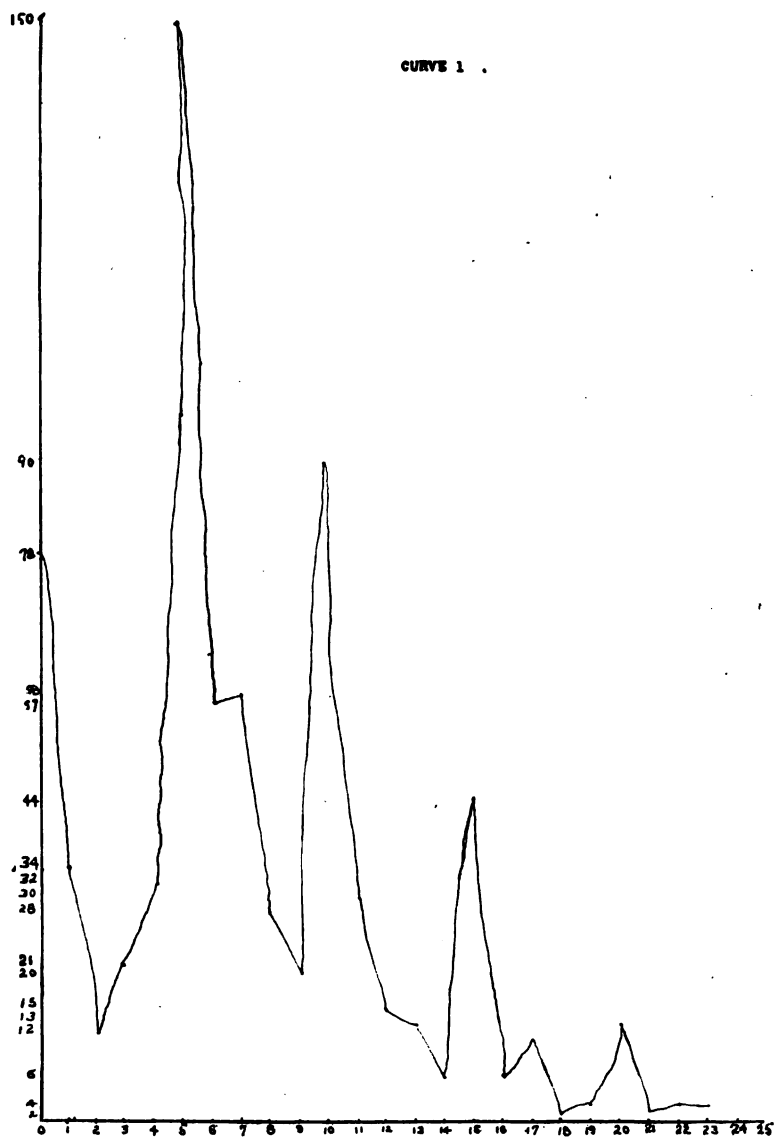
TABLE I.

AMOUNT OF ERROR IN MILLIMETERS	NUMBER OF TIMES
0	78
1	34
2	12
3	21
4	32
5	150
6	57
7	58
8	28
9	20
10	90
11	30
12	15
13	13
14	6
15	44
16	6
17	11
18	1
19	2
20	13
21	1
22	2
23	2
Total . . . . .	726

TABLE II.

DIRECTION OF ERROR	NUMBER OF TIMES
Down . . . . .	202
Up . . . . .	41
Right . . . . .	101
Left . . . . .	33
Down and Right	192
Down and Left	35
Up and Left . . .	14
Up and Right . .	27
Total . . . . .	645

In curve 1, which shows the distribution of the frequency of the errors, the numbers along the abscissa represent the amount of the errors in millimeters, while those along the ordinate represent the number of times the error was made, every milli-



meter representing one trial. All the other curves representing the distribution of the frequency of the errors were drawn in a similar manner. In every case the numbers on the abscissa were separated by a space of four millimeters.

Curves showing the distribution of the direction of the error will be discussed in the second part of this paper.

From a consideration of curve 1, and from actual observations of the errors made by the subject when different parts of the square were touched, it was evident that there were at least three distinct areas within the square in which the subject's localization power differed markedly. The largest errors were made when points in the upper part of the square were touched, and in curve 1 this area would be represented by a perpendicular erected at 10. The middle area would be represented by a perpendicular erected at 5. The subject was most accurate in the lowest part of the square. Here his error seldom exceeded 5 millimeters, and this area is responsible for the height of the curve at 0.

Therefore, in order to make the work more accurate and uniform, the square was divided into the areas A, B, and C (Fig. 1). Area A included that part of the square between columns 1 and 3; Area B, that part between columns 3 and 6, and area C, that part between columns 6 and 7. Thereafter, all the results were tabulated according to columns, these columns being later grouped into their respective areas.

Several hundred experiments were then made in the same manner as described above, but were tabulated according to the new method. Tables III and IV give the records of these experiments. From the data of table III we find the average errors and the average variations for the three areas to be as follows:

AREA	AVERAGE ERROR	AVERAGE VARIATION
A	7	2.5
B	4.2	1.2
C	2.7	1.3

We see from these figures that the average error decreases, or, in other words, that the subject's localization ability increases as we pass from area A to C, thus confirming the deduction made above from curve 1. Curves 2, 3, and 4 bring this



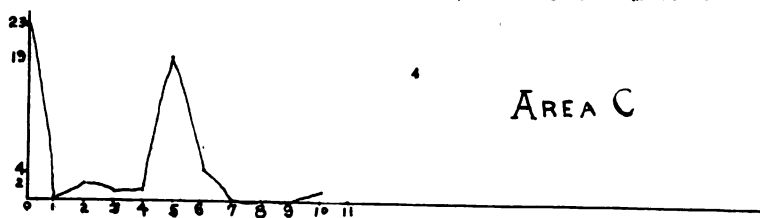
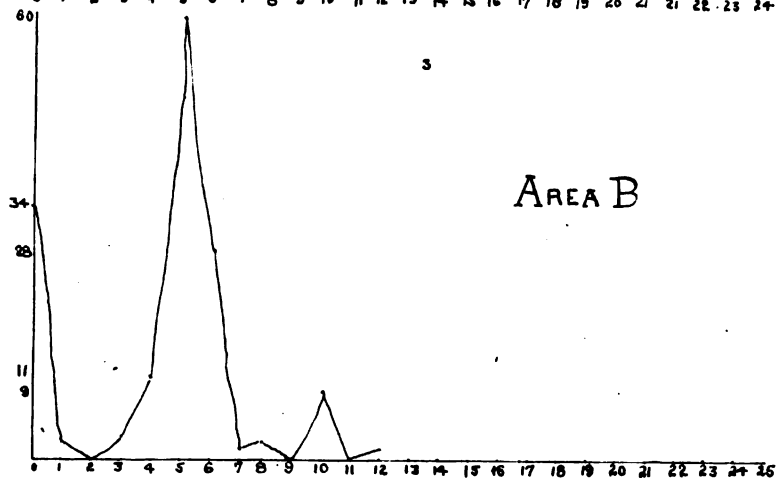
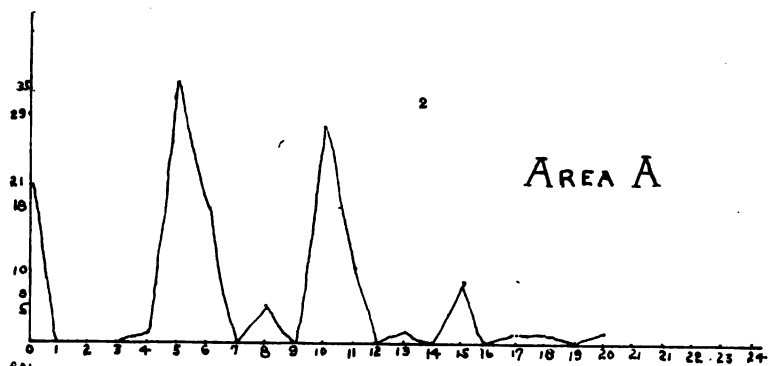
fact out still more clearly. In Area A, although the mode is at 5, the median lies between 5 and 10; in area B, the mode is at 5 and the median at 4.2, and in area C, the mode is at 0 and the median at .5. As we pass from area A to area C we also notice that the errors become smaller and smaller, being as high as 20 millimeters in area A and not exceeding 6 millimeters, with but one exception, in area C. This fully justifies our somewhat arbitrary division of the square into three distinct areas.

TABLE III.

AMOUNT OF ERROR IN  <i>mm.</i>	NUMBER OF TIMES									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
0	6	8	7	21	9	12	13	34	23	23
1	..	..	..	..	..	1	1	2	..	..
2	..	..	..	..	..	..	..	..	2	2
3	..	..	..	..	2	1	..	3	1	1
4	..	..	1	1	3	5	3	11	1	1
5	10	8	17	35	20	18	22	60	19	19
6	3	6	9	18	13	5	10	28	4	4
7	..	..	..	..	..	1	..	1	..	..
8	3	1	1	5	2	..	..	2	..	..
9	..	..	..	..	..	..	..	..	..	..
10	13	10	6	29	4	4	1	9	1	1
11	3	5	2	10	..	..	..	..	..	..
12	..	..	..	..	..	1	..	1	..	..
13	..	1	..	1	..	..	..	..	..	..
14	..	..	..	..	..	..	..	..	..	..
15	5	2	1	8	..	..	..	..	..	..
16	..	..	..	..	..	..	..	..	..	..
17	1	..	..	1	..	..	..	..	..	..
18	1	..	..	1	..	..	..	..	..	..
19	..	..	..	..	..	..	..	..	..	..
20	..	1	..	1	..	..	..	..	..	..
Total,	..	..	..	131	..	..	..	151	..	51

TABLE IV.

DIRECTION OF ERROR	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6			
Up ....	..	1	..	1	3	6	2	11	9	9
Up and Right...	..	..	1	1	1	2	..	3	..	..
Right ....	..	..	3	3	6	6	4	16	6	6
Down and Right...	2	4	..	6	6	1	9	16	..	..
Down ..	29	21	22	72	19	11	12	42	1	1
Down and Left.	7	6	7	20	7	6	4	17	..	..
Left ....	..	1	2	3	..	2	3	5	8	8
Up and Left ....	..	..	..	..	2	2	1	5	7	7
Total	..	..	..	106	..	..	..	115	..	31



## Experiment No. 2.

In this experiment the subject's middle finger was clamped to the table and the screw adjusted until the stimulus was a little short of being very painful, or equivalent to 5 when measured on Cattell's algometer. The distance of the clamp from the lower border of the square was about 7 centimeters (*T*, *Fig. 1*). The subject closed his eyes, and the same procedure as in experiment No. 1 was followed. During the trials the screw was always re-adjusted so as to keep the intensity of the constant stimulus uniform throughout. Tables V and VI show the results of several hundred trials.

If we compare curves 5, 6, and 7, which show the distribution of the frequency of the errors for the three areas, with the normal curves 2, 3, and 4, respectively, we find that area A, instead of having the crest of the curve at 5, as is true of the normal, has the crest at 10. This means that the mode has changed from 5 to 10, and that the median has shifted from 5.5 to 6.9. The difference is more marked when we compare curves 3 and 6. The relative heights of the curve at 0 and at 5 in the former is, roughly speaking, as 1:2; in the latter the proportion is as 1:3. This shows a marked decrease in the subject's accuracy of judgment. The median has been pulled from 4.2 to 4.8. The decrease in the accuracy of localization becomes very evident on comparison of curve 4 with curve 7. In the first place, while in the normal trials the subject never, with but one exception, made an error greater than 6 millimeters, in the presence of the constant stimulus his errors varied from 1 to 21 millimeters. In the second place, the mode changed from 0 to 5 millimeters, and, lastly, the median jumped from .5 to 4.4.

These differences stand out even more prominently when we contrast the average errors and average variations in the two experiments. The average errors and average variations for the three areas in this experiment are:

AREA	AVERAGE ERROR	AVERAGE VARIATION
A	7.6	3
B	6	2.2
C	5.4	2.3

Comparing these figures with those given under experiment No. 1, we find that the average error in area A has increased .6, in B, 1.8, and in C, 2.7. That is, the closer the area to the

other words, the closer the area to the constant stimulus, the greater the decrease in the subject's ability of localization.

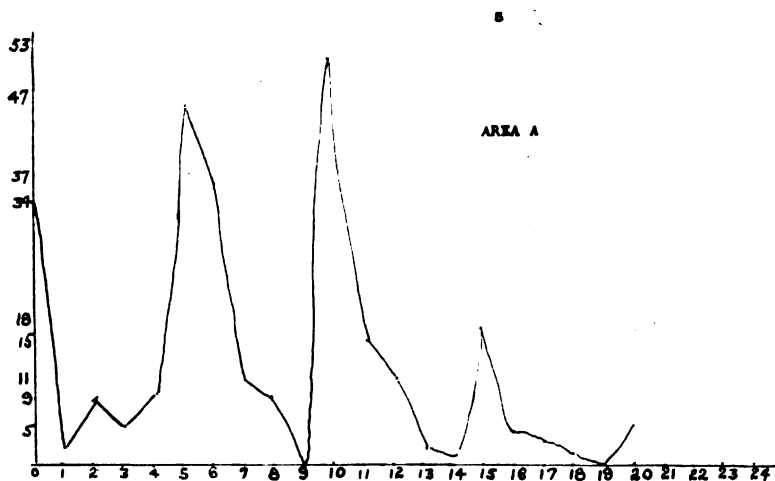
TABLE V.

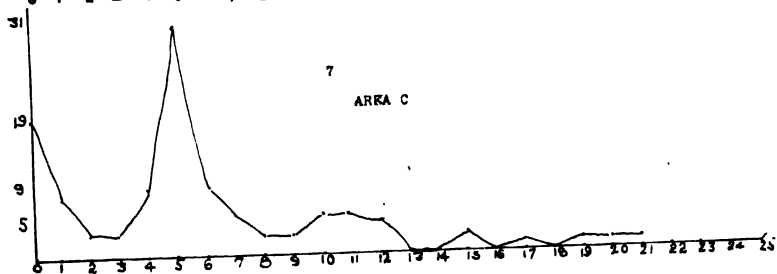
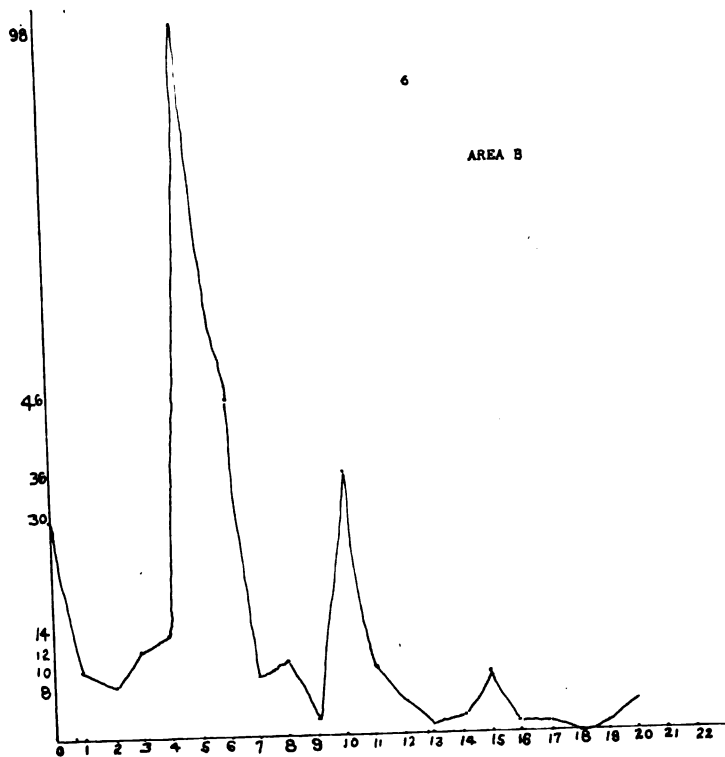
AMOUNT OF ERROR IN <i>mm.</i>	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
0	11	5	18	34	13	12	5	30	19	19
1	1	..	1	2	2	2	5	9	8	8
2	..	3	5	8	2	2	3	7	3	3
3	2	2	1	5	4	7	1	12	3	3
4	3	3	3	9	4	4	6	14	9	9
5	15	19	13	47	26	29	43	98	31	31
6	9	16	12	37	15	14	17	46	9	9
7	2	6	3	11	1	3	4	8	5	5
8	7	..	2	9	3	4	3	10	2	2
9	..	..	..	..	1	1	..	2	2	2
10	23	16	14	53	15	16	5	36	5	5
11	7	4	5	16	2	4	3	9	5	5
12	1	8	2	11	1	2	1	4	4	4
13	1	..	1	2	..	..	1	1	..	..
14	..	..	1	1	..	2	..	2	..	..
15	7	6	5	18	3	2	3	8	2	2
16	..	3	1	4	..	..	1	1	..	..
17	1	1	1	3	1	..	..	1	1	1
18	..	..	1	1	..	..	..	..	..	..
19	..	..	..	..	..	..	1	1	1	1
20	2	1	2	5	1	2	1	4	1	1
Total,	..	..	..	276	..	..	..	303	..	110



TABLE VI.

DIRECTION OF ERROR	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
Up . . . .	..	8	10	18	16	16	25	57	31	31
Up and										
Right . . .		4	..	4	5	2	3	10	9	9
Right . . .	9	5	6	20	6	7	4	17	11	11
Down										
and										
Right . . .	13	19	7	39	3	7	5	15	1	1
Down . .	40	27	40	107	27	23	25	75	2	2
Down										
and Left	14	19	10	43	9	8	4	21	1	1
Left . . .	4	3	4	11	14	21	12	47	20	20
Up and										
Left . . .	..	2	2	4	8	9	11	28	19	19
Total,	..	..	..	246	..	..	..	270	..	94





### Experiment No. 3.

The clamp was placed about 2 centimeters to the right (subject's) of the square on a level with columns 5, 6, and 7 (*R*, *Fig. 1*). The screw was adjusted until the intensity of the stimulus was equal to that used in experiment No. 2. The same mode of operation as in the previous experiments was followed. Tables VII and VIII give the records of the results. Curves 8, 9, and 10 were drawn similar to the preceding curves. Comparing these with the normal curves, we find that in area A the median has changed from 5.5 to 6.3; in area B, from 4.2 to 4.8, and in area C, from .5 to 4.4. In the latter case the mode has also changed, jumping from 0 to 5 millimeters. The average errors and average variations for this experiment are:

AREA	AVERAGE ERROR	AVERAGE VARIATION
A	8.4	3.7
B	5.8	2
C	4.2	1.6

Comparing these figures with those of the normal, as given under experiment 1, we find that the average error of area A has increased 1.4; that of area B, 1.6, and that of area C, 1.5. At first sight these figures do not seem to bear out the deduction made above, namely, that the nearer the area to the constant stimulus, the greater the increase in the error. It should be remembered, however, that in the former case the constant stimulus was applied about 7 centimeters from the lower border of the square, while in the latter it was applied about 2 centimeters to the right of the square and almost equally distant from the three areas. Consequently, in the latter case the distracting influence of the constant stimulus will be distributed more uniformly over the various areas and the differences in the increase of the errors for the three areas will not be so marked, a condition borne out by the figures.

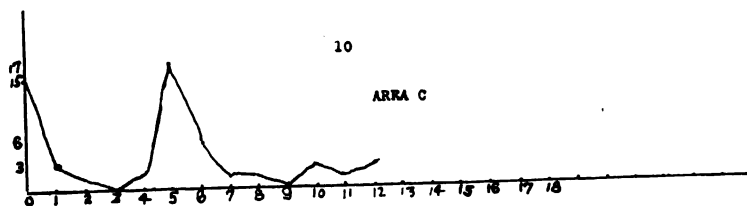
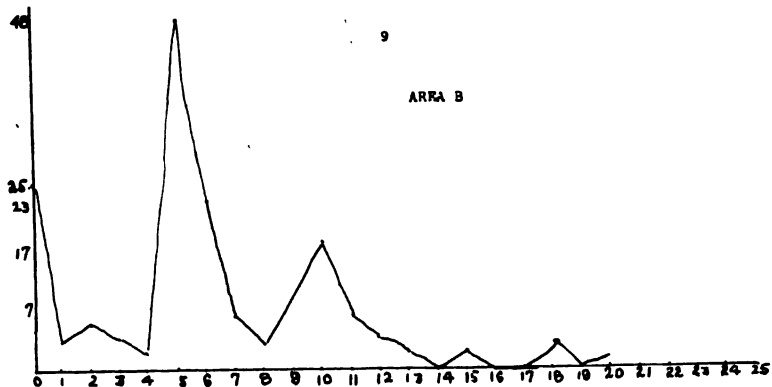
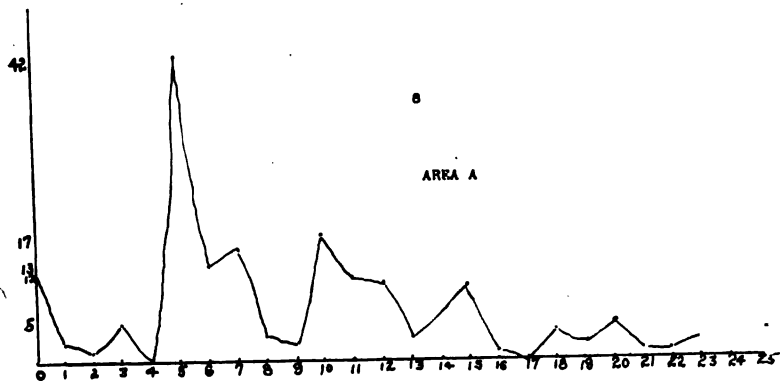
TABLE VII.

AMOUNT OF ERROR IN mm.	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
0	4	3	5	12	4	10	11	25	15	15
1	..	..	2	2	1	1	2	4	3	3
2	1	..	..	1	3	1	2	6	1	1
3	2	3	..	5	1	..	3	4	..	..
4	..	..	..	..	1	..	1	2	2	2
5	10	15	17	42	18	12	18	48	17	17
6	1	5	7	13	5	9	9	23	6	6
7	2	2	11	15	2	2	3	7	1	1
8	2	1	..	3	1	1	1	3	1	1
9	1	1	..	2	..	..	..	..	..	..
10	7	5	5	17	8	9	..	17	3	3
11	1	3	7	11	4	3	..	7	1	1
12	1	6	3	10	..	3	1	4	3	3
13	2	1	..	3	..	1	1	2	..	..
14	..	..	..	..	..	..	..	..	..	..
15	1	3	6	10	..	..	2	2	..	..
16	1	..	..	1	..	..	..	..	..	..
17	..	..	..	..	..	..	..	..	..	..
18	3	..	1	4	2	..	1	3	..	..
19	1	1	..	2	..	..	..	..	..	..
20	4	..	1	5	..	1	..	1	..	..
21	1	..	..	1	..	..	..	..	..	..
22	..	1	..	1	..	..	..	..	..	..
23	2	..	..	2	..	..	..	..	..	..
Total,	..	..	..	162	..	..	..	158	..	53



TABLE VIII.

DIREC- TION OF ERROR	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
Up ....	3	3	1	7	4	2	7	13	7	7
Up and Right...	..	..	3	3	5	5	4	14	4	4
Right...	5	4	3	12	3	11	7	21	11	11
Down and Right...	16	13	13	42	..	6	6	12	..	..
Down ..	16	18	17	51	18	10	4	32	1	1
Down and Left.	2	5	3	10	7	2	3	12	1	1
Left ...	1	1	6	8	6	3	5	14	8	8
Up and Left ...	..	..	..	..	1	3	5	9	5	5
Total,	..	..	..	133	..	..	..	127	..	37



#### Experiment No. 4.

The purpose of this experiment was to see whether the subject still retained his normal ability of touch localization. This experiment was carried out in exactly the same manner as experiment No. 1. Not many trials were made, as the results seemed, with slight variation, to agree with those of the normal. Tables IX and X give the records of several hundred trials. Curves 11, 12, and 13 agree in general with curves 2, 3, and 4. A comparison of the medians follows:

	AREA A	AREA B	AREA C
1st Normal .....	5.5	4.2	.5
2d Normal .....	5.8	4.6	.3

A comparison of the average errors and average variations gives about the same results.

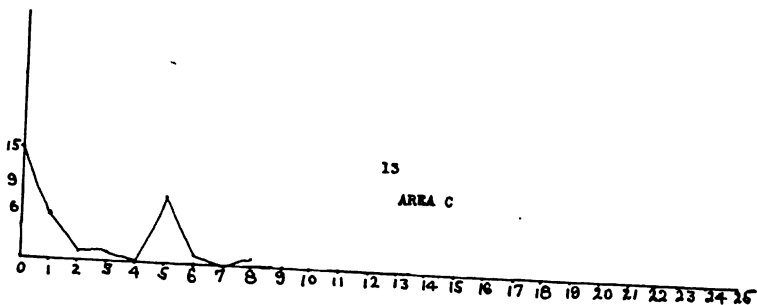
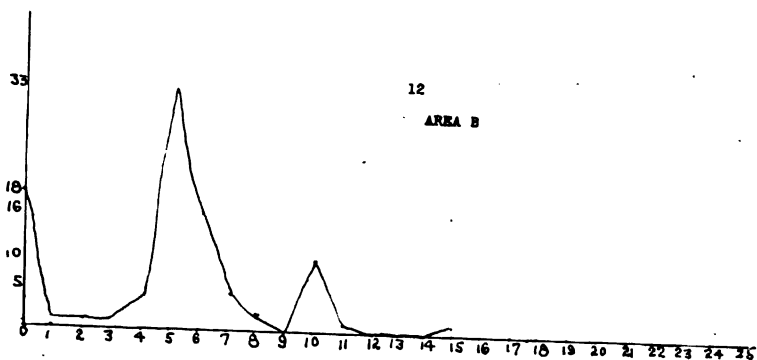
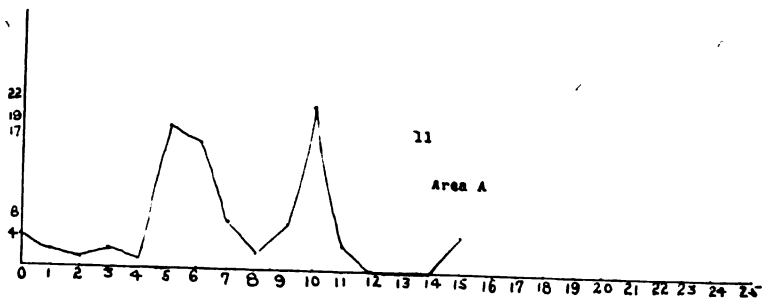
	AREA A		AREA B		AREA C	
	AVER. ERROR	AVER. VARIA- TION	AVER. ERROR	AVER. VARIA- TION	AVER. ERROR	AVER. VARIA- TION
1st Normal—	7	2.5	4.2	1.2	2.7	1.3
2d Normal—	7.1	2.4	4.9	1.2	2	1.2

TABLE IX.

AMOUNT OF ERROR IN <i>mm.</i>	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
0	..	..	4	4	5	10	3	18	15	15
1	..	1	1	2	..	1	..	1	6	6
2	1	..	..	1	..	1	..	1	1	1
3	..	2	..	2	1	..	..	1	1	1
4	1	..	..	1	1	1	2	4	..	..
5	6	7	6	19	7	10	16	33	9	9
6	7	3	7	17	5	5	6	16	1	1
7	3	2	1	6	4	..	1	5	..	..
8	1	1	..	2	..	1	1	2	1	1
9	2	2	2	6	..	..	..	..	..	..
10	3	7	10	20	6	4	..	10	..	..
11	2	1	..	3	..	..	1	1	..	..
12	..	..	..	..	..	..	..	..	..	..
13	..	..	..	..	..	..	..	..	..	..
14	..	..	..	..	..	..	..	..	..	..
15	2	3	..	5	1	..	..	1	..	..
Total,	..	..	..	88	..	..	..	93	..	34

TABLE X.

DIRECTION OF ERROR	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
Up ....	..	..	3	3	2	1	3	6	3	3
Up and Right...	..	..	4	4	..	3	2	5	1	1
Right...	5	3	5	13	3	9	4	16	11	11
Down and Right...	14	8	5	27	4	1	5	10	..	..
Down ..	6	14	9	29	12	8	10	30	1	1
Down and Left.	1	3	..	4	1	1	1	3	..	..
Left ....	1	2	1	4	..	..	1	1	2	2
Up and Left ....	..	..	..	..	1	..	1	2	1	1
Total,	..	..	..	84	..	..	..	73	..	19



### Experiment No. 5.

The clamp was placed about 2 centimeters to the left (subject's) of the outer margin of the square, on a level with columns 5, 6, and 7 (*L, Fig. 1*), a position almost directly opposite to that of the clamp in experiment No. 3. The screw was adjusted until the intensity of the stimulus was the same as that used in the preceding experiments and the same method was followed. The results as given in tables XI and XII are, in general, analogous to those of experiments 2 and 3. Curves 14, 15, and 16, which represent the distribution of the frequency of the errors, bear the same comparison with curves 2, 3, and 4, the normal curves, as do curves 8, 9, and 10 of experiment No. 3, where the constant stimulus was applied to the right of the square. The medians have changed in almost the same amounts as did those of experiment No. 3, and in area C the mode has also changed similarly. From table XI we also find that there has been an increase in the amount of the errors, this increase being as great as 12 millimeters in area C. A comparison of the medians, average errors, and the average variations of this experiment, with those of the normal, follows:

#### MEDIANS.

	AREA A	AREA B	AREA C
Normal .....	5.5	4.2	.5
Stimulus to left .....	6.3	5.7	5.6

	AREA A		AREA B		AREA C	
	AVER. ERROR	AVER. VARIATION	AVER. ERROR	AVER. VARIATION	AVER. ERROR	AVER. VARIATION
Normal .....	7.	2.5	4.2	1.2	2.7	1.3
Stimulus to left .....	8.1	3.2	7.7	2.7	6.3	2.6

Thus we see that in area A, that part of the square farthest away from the constant stimulus, the increase in the amount of the error is smaller than in areas B and C. This is in line with the results obtained in experiments No. 2 and No. 3.

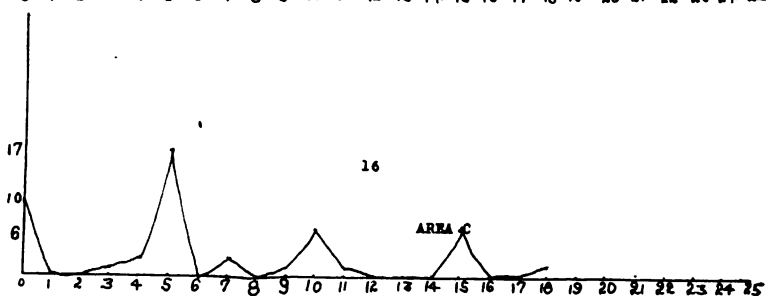
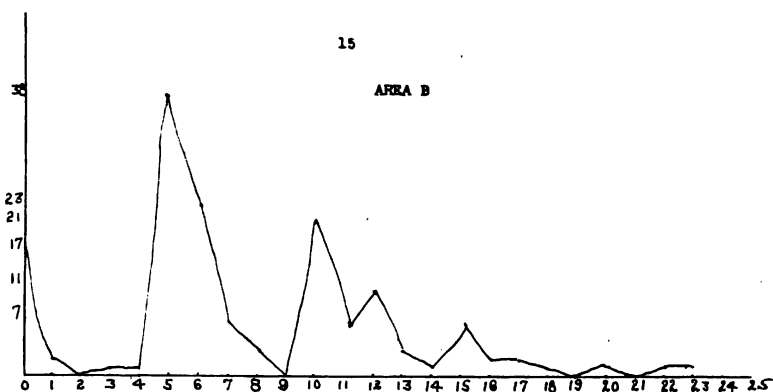
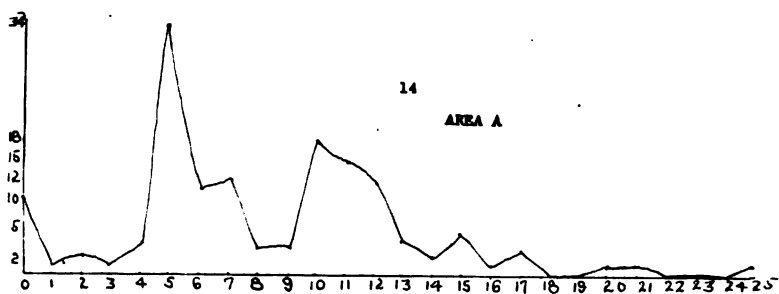
TABLE XI.

AMOUNT OF ERROR IN <i>mm.</i>	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
0	..	6	4	10	8	5	4	17	10	10
1	..	..	1	1	1	1	..	2	..	..
2	..	2	..	2	..	..	..	..	..	..
3	..	1	1	2	..	..	1	1	1	1
4	..	..	4	4	1	..	..	1	2	2
5	12	11	11	34	10	15	13	38	17	17
6	1	2	8	11	5	6	12	23	..	..
7	2	6	4	12	..	2	5	7	2	2
8	..	2	1	3	2	..	1	3	..	..
9	2	..	1	3	4	10	7	21	1	1
10	6	6	6	18	2	2	3	7	6	6
11	8	5	2	15	4	3	4	11	1	1
12	5	4	3	12	2	1	..	3	..	..
13	2	1	1	4	..	1	..	1	..	..
14	2	..	..	2	4	2	1	7	..	..
15	1	3	1	5	2	..	..	2	6	6
16	1	..	..	1	2	..	..	2	..	..
17	1	1	1	3	..	1	..	1	..	..
18	..	..	..	..	..	..	..	..	1	1
19	..	..	..	..	..	..	..	..	..	..
20	..	..	1	1	1	..	..	1	..	..
21	1	..	..	1	..	..	..	..	..	..
22	..	..	1	1	1	..	..	1	..	..
23	..	..	..	..	1	..	..	1	..	..
24	..	..	..	..	..	..	..	..	..	..
25	1	..	..	1	..	1	..	1	..	..
Total,	..	..	..	146	..	..	..	151	..	47



TABLE XII.

DIREC- TION OF ERROR	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
Up ....	..	..	..	..	..	5	5	10	2	2
Up and Right...	..	4	4	8	..	3	..	3	3	3
Right...	5	1	12	18	8	10	10	28	27	27
Down and Right...	15	11	10	36	13	10	12	35	..	..
Down ..	15	30	13	58	15	12	5	32	..	..
Down and Left.	8	4	4	16	2	2	1	5	2	2
Left ....	2	4	2	8	3	2	5	10	4	4
Up and Left ...	..	..	2	2	2	1	5	8	..	..
Total,	..	..	..	146	..	..	..	131	..	38



### Experiment No. 6.

In this experiment a square, corresponding in size and position to the one on the subject's left hand, was marked off on his right hand. The subject closed both eyes and was touched lightly with two pressure points on corresponding points of the two squares. Then he was asked to locate the spot touched on his left hand, the hand upon which all the previous experiments had been made. Equal pressure upon the corresponding points was kept, as far as possible, and those cases where it was obvious that one of the points had been touched with greater force than the other were thrown out. The purpose of this experiment was to see if the stimulation of corresponding points would increase the subject's ability to localize touches, or if it would have the same effect as the presence of a constant stimulus. The results of almost seven hundred trials, as given in tables XIII and XIV and as diagrammatically represented in curves 17, 18, and 19, would seem to show that the stimulation of corresponding points had neither of the effects above mentioned. Its effect, at most, seemed rather to be that of a weak disturbing element. Although the corresponding points were stimulated practically simultaneously, the subject claimed that he always felt two distinct sensations. There was, however, a greater feeling of "oneness," a more perfect blending of the sensations, when two corresponding points were simultaneously stimulated than when two non-corresponding points, such as, for example, a point in column 6, and a point in column 5, were simultaneously stimulated. The medians of areas A and B differ very little from those of the first normal and are exactly the same as those of the second normal. Area C, however, for some unaccountable reason, shows a marked difference, jumping from .5 to 3.5. The average errors show a small increase for all three areas.

#### MEDIANS.

	AREA A	AREA B	AREA C
1st Normal .....	5.5	4.2	.5
2d Normal .....	5.8	4.6	.3
Corresponding points ...	5.8	4.6	3.5

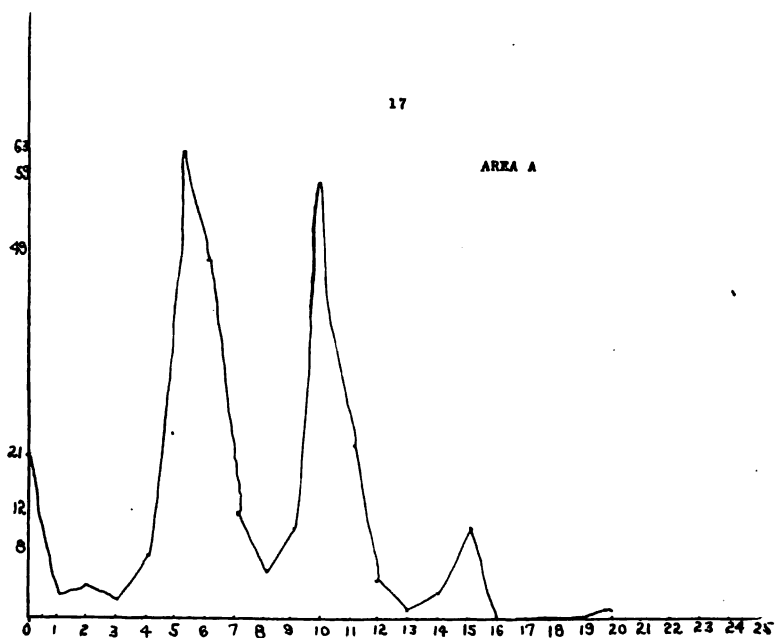
	AREA A		AREA B		AREA C	
	AVER. ERROR	AVER. VARIATION	AVER. ERROR	AVER. VARIATION	AVER. ERROR	AVER. VARIATION
1st Normal ..	7	2.5	4.2	1.2	2.7	1.3
2d Normal ..	7.1	2.4	4.9	1.2	2	1.2
Corresponding points.	7.2	2.4	5.5	1.6	3.1	1.4

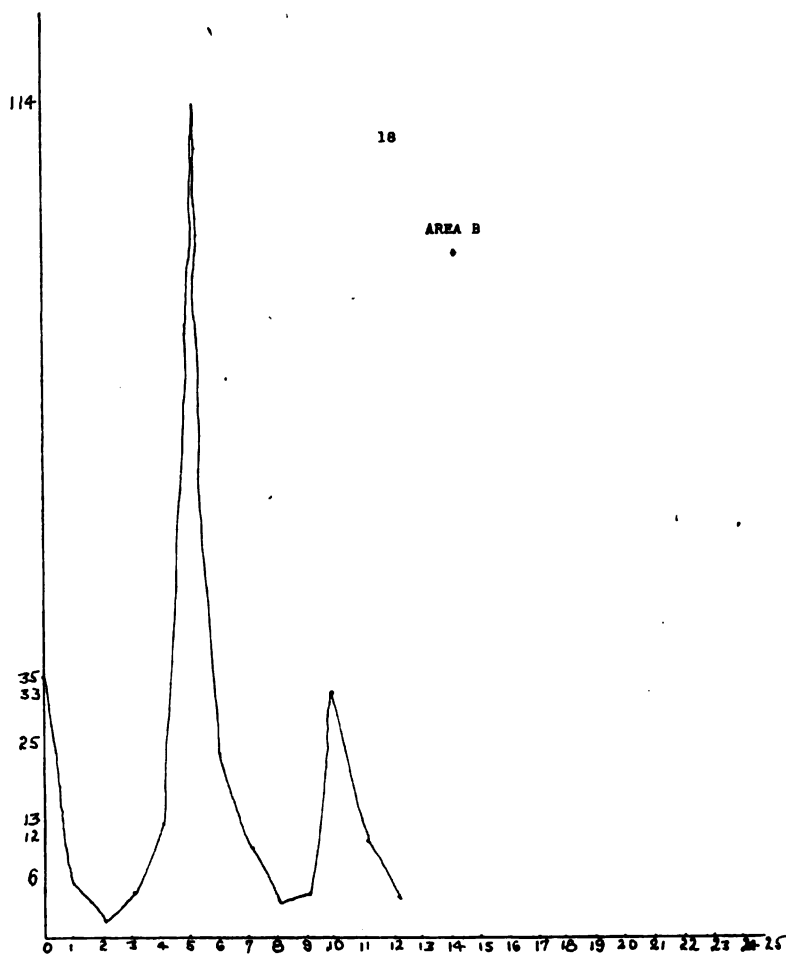
TABLE XIII.

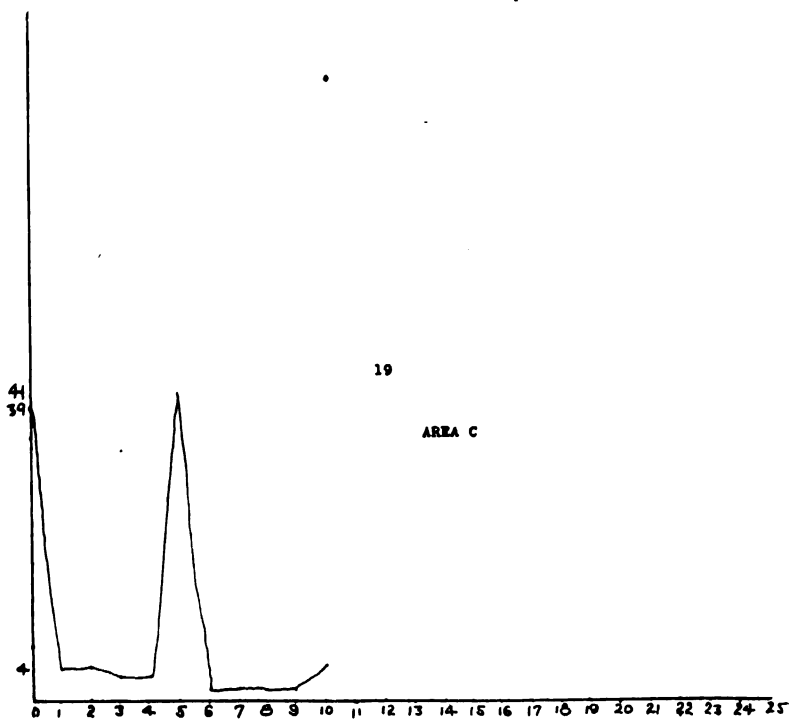
AMOUNT OF ERROR IN mm.	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C.	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
0	11	5	5	21	11	11	13	35	39	39
1	2	..	1	3	2	2	3	7	4	4
2	3	1	..	4	1	..	1	2	4	4
3	2	..	..	2	1	3	2	6	3	3
4	2	3	3	8	2	4	7	13	3	3
5	20	20	23	63	33	38	43	114	41	41
6	11	15	23	49	12	7	6	25	1	1
7	5	5	4	14	6	4	2	12	1	1
8	1	2	3	6	3	2	..	5	1	1
9	7	4	1	12	2	2	2	6	1	1
10	19	21	19	59	15	13	5	33	4	4
11	6	9	8	23	8	3	2	13	1	1
12	2	1	2	5	2	3	..	5	..	..
13	1	..	..	1	..	..	..	..	..	..
14	1	1	1	3	..	..	..	..	..	..
15	5	4	3	12	..	..	..	..	..	..
16	..	..	..	..	..	..	..	..	..	..
17	..	..	..	..	..	..	..	..	..	..
18	..	..	..	..	..	..	..	..	..	..
19	..	..	..	..	..	..	..	..	..	..
20	..	..	1	1	..	..	..	..	..	..
Total	..	..	..	286	..	..	..	276	..	103

TABLE XIV.

DIRECTION OF ERROR	NUMBER OF TIMES.									
	AREA A				AREA B				AREA C	
	COLUMNS			TOTAL	COLUMNS			TOTAL	COL.	TOTAL
	1	2	3		4	5	6		7	
Up ....	1	1	1	3	2	4	6	12	10	10
Up and Right ...	..	3	4	7	5	4	..	9	1	1
Right ...	11	13	15	39	14	9	15	38	24	24
Down and Right ...	26	25	26	77	24	13	15	52	..	..
Down ..	46	35	32	113	32	40	31	103	5	5
Down and Left.	9	6	11	26	5	9	7	21	..	..
Left ...	..	..	1	1	..	2	7	9	23	23
Up and Left ...	..	1	..	1	..	1	..	1	3	3
Total,	..	..	..	267	..	..	..	245	..	66









## SUMMARY.

Probably the most concise way to summarize the results of the previous experiments is to make comparative tables of the medians, average errors, and average variations. Such tables show, almost at a glance, what can be logically inferred from the work.

**COMPARATIVE TABLE OF THE MEDIANS.**

	AREA A	AREA B	AREA C
1st Normal .....	5.5	4.2	.5
Constant Stimulus applied to tip of middle finger ....	6.9	4.8	4.4
Constant Stimulus applied to right of square .....	6.3	4.8	4.3
2d Normal .....	5.8	4.6	.3
Constant Stimulus applied to left of square .....	6.3	5.7	5.6
Stimuli applied to corresponding points ...	5.8	4.6	3.5

In all cases where the constant stimulus was applied there was a marked increase in the median, especially in area C, where the subject's ability to localize touches was the greatest.

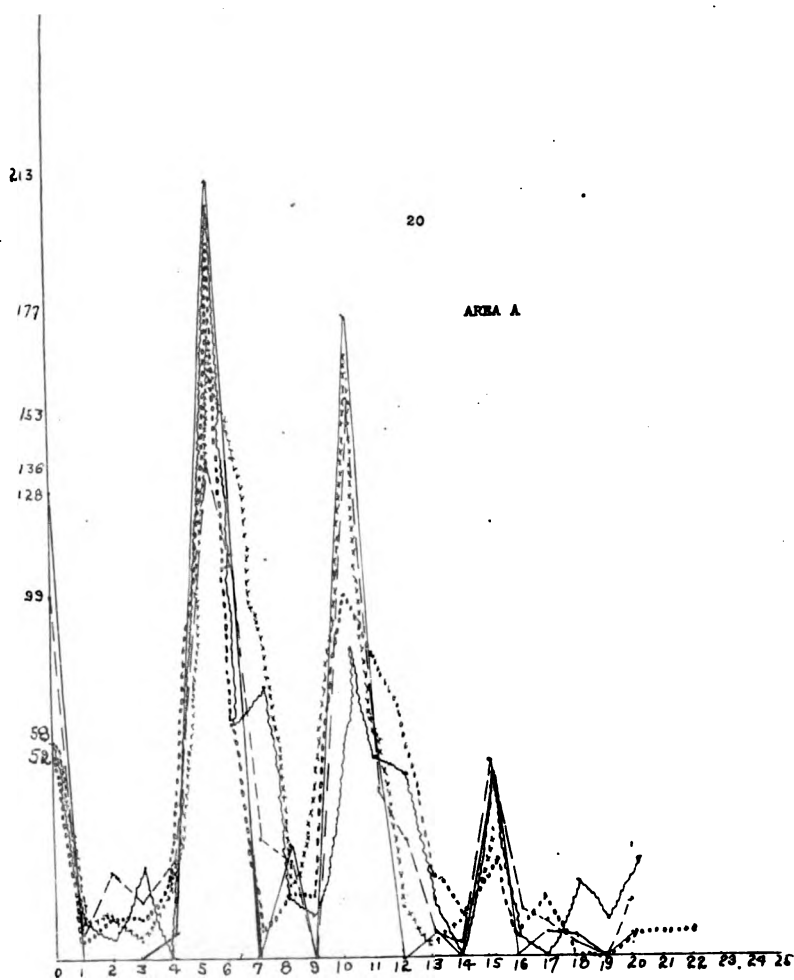
**COMPARATIVE TABLE OF THE AVERAGE ERRORS AND  
AVERAGE VARIATIONS.**

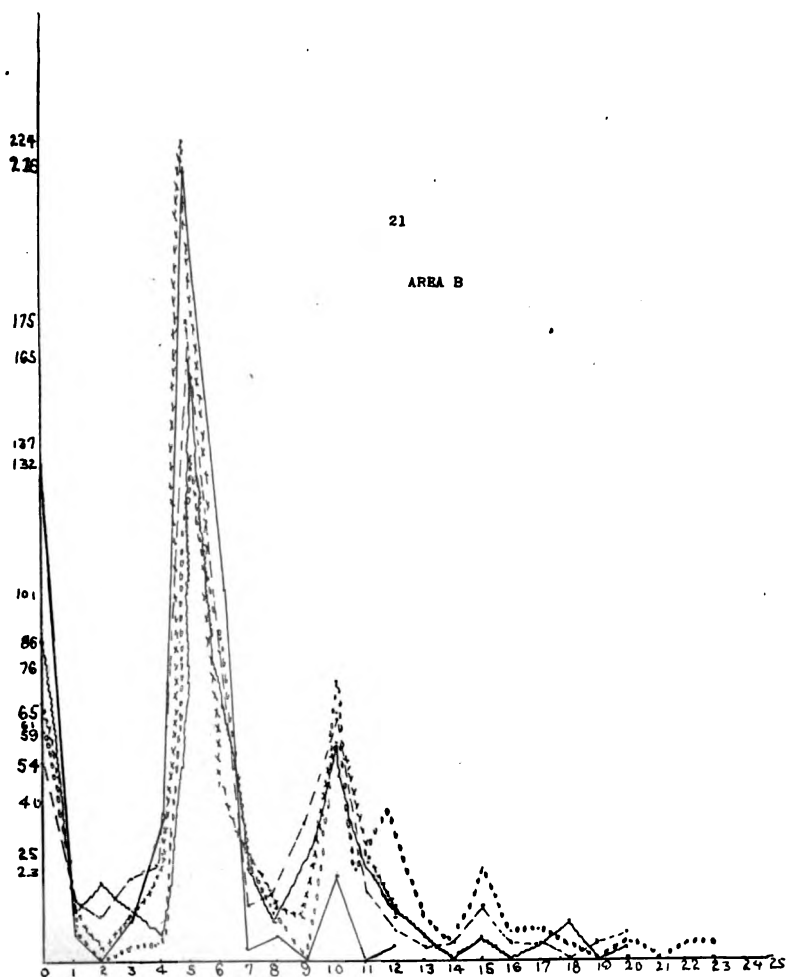
	AREA A		AREA B		AREA C	
	AVER. ERROR	AVER. VARIA- TION	AVER. ERROR	AVER. VARIA- TION	AVER. ERROR	AVER. VARIA- TION
1st Normal..	7	2.5	4.2	1.2	2.7	1.3
Constant Stimulus applied to tip of middle finger .....	7.6	3	6	2.2	5.4	2.3
Constant Stimulus applied to right of square .....	8.4	3.7	5.8	2	4.2	1.6
2d Normal ..	7.1	2.4	4.9	1.2	2	1.2
Constant Stimulus applied to left of square .....	8.1	3.2	7.7	2.7	6.3	2.6
Stimuli applied to correspond- ing points .....	7.2	2.4	5.5	1.6	3.1	1.4

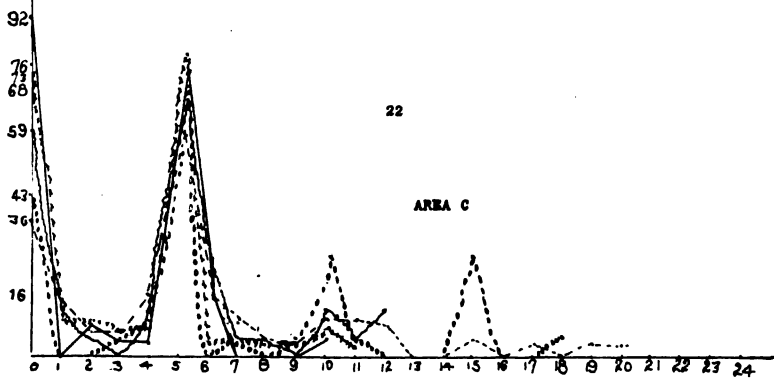
By reducing the cases of all the experiments to the same total number, it was possible to construct the composite curves 20, 21, and 22. Every millimeter on the ordinate is equivalent to two cases. In these curves the straight line represents the first experiment; the broken line, the second; the irregular line, the third; the circles, the fifth; and the crosses, the sixth. These curves show very plainly the increase in the amount of the errors in the presence of the constant stimulus, an increase which becomes more and more pronounced as we pass from the curves representing area A to those representing area C.

During all the trials the subject naturally concentrated his attention upon the sensation from the pressure point and subordinated the continuous sensation derived from the constant stimulus as much as the pain from the latter would permit.

The results of these experiments would seem to show, however, that unconsciously, at least, the subject's attention vacillated, now focalizing the sensations from the pressure point, and now those from the clamp. This subconscious attention to the constant stimulus interfered a good deal with the subject's accuracy of perception, as can readily be seen from the tables and curves. That the influence of the constant stimulus was non-voluntary and subconscious is proved by the fact that the subject was just as positive about the correctness of his localizations in the trials when the constant stimulus was applied as in the normal trials. There was just as little uncertainty and hesitancy in the one case as in the other. In other words, to the subject it seemed that, although the clamp was inconvenient and somewhat painful, it did not in the least affect his ability to localize. As far as he was aware, he was irresponsive to the continuous sensations from the clamp.





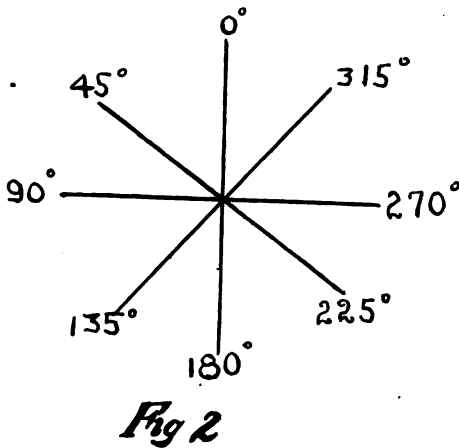


## Part II:

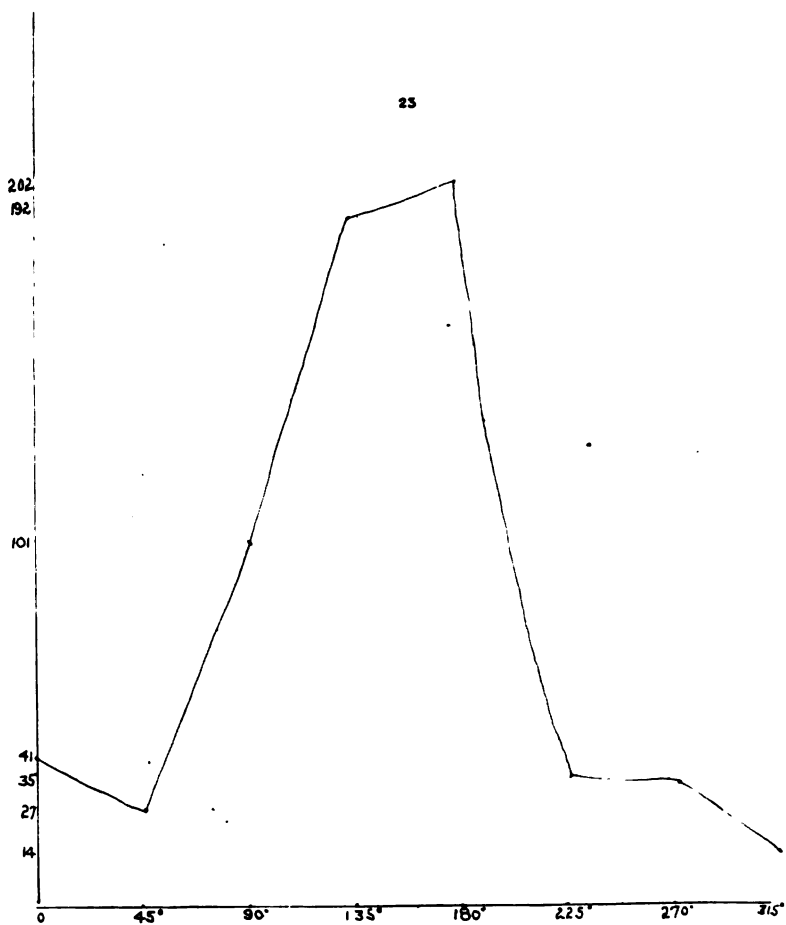
### CONSIDERATIONS OF THE DIRECTION OF ERRORS.

So far we have considered only the effect of the constant stimulus upon the amount of the error. Let us now consider what influence, if any, the constant stimulus exerted upon the direction of the error.

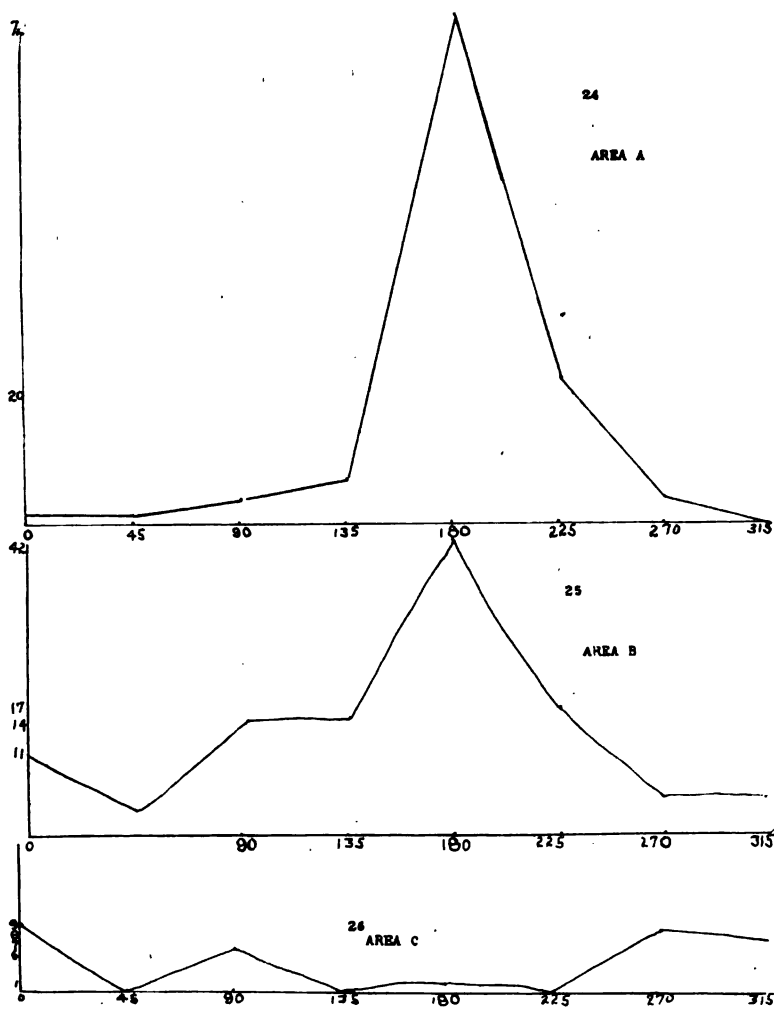
Curves 23 to 32, inclusive, were constructed from the data furnished by tables II, IV, VI, VIII, X, XII, and XIV, respectively, in the following manner: Two lines were drawn perpendicular to each other. Passing through their point of intersection, and bisecting the right angles, were drawn two diagonals (*Fig. 2*). Beginning with the upper vertical line and letting it represent the "ups" or errors made above the point stimulated and passing toward the right (subject's), each line was made to represent a certain direction. For the sake of clearness and simplicity each line was labeled by the number of degrees in the arc it intercepted. Thus we have:



- 0°=up.  
45°=up and to the right.  
90°=right.  
135°=down and to the right.  
180°=down.  
225°=down and to the left.  
270°=left.  
315°=up and to the left.  
In all the curves representing the distribution of the direc-





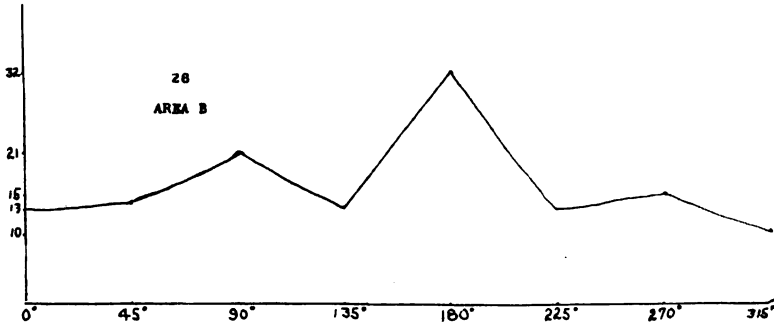
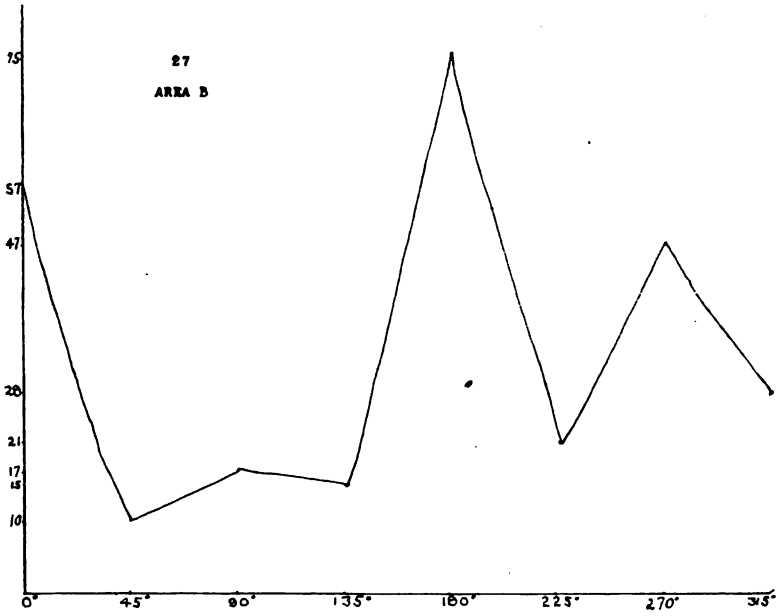


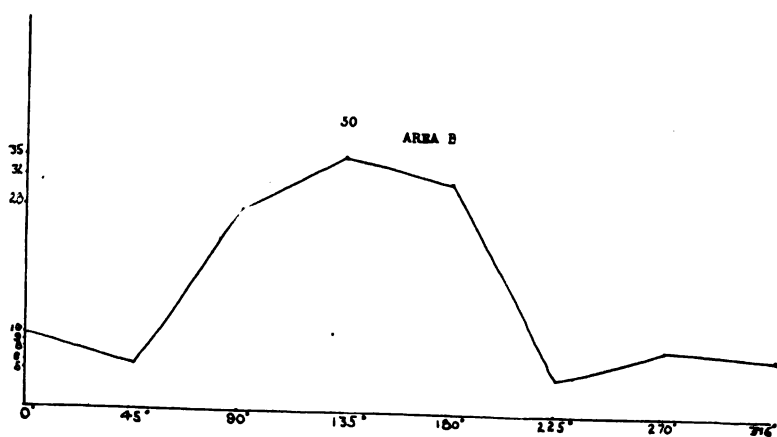
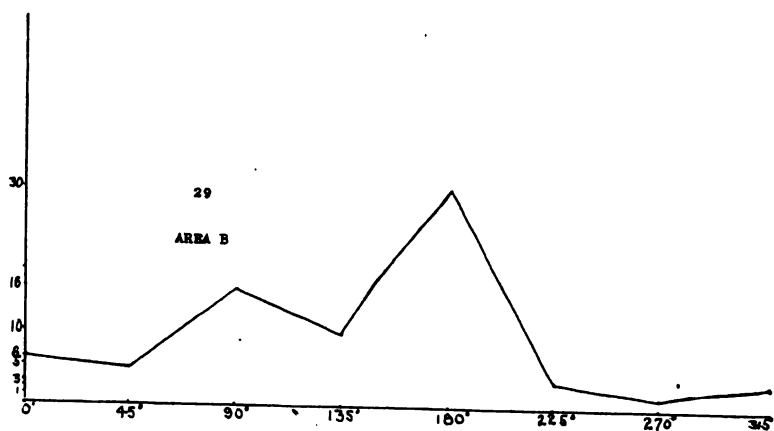
tion of the errors, one-third of a millimeter on the abscissa is equivalent to one degree, and every millimeter on the ordinate is equivalent to one case. In curves 23 and 32, however, every half millimeter on the ordinate represents one case.

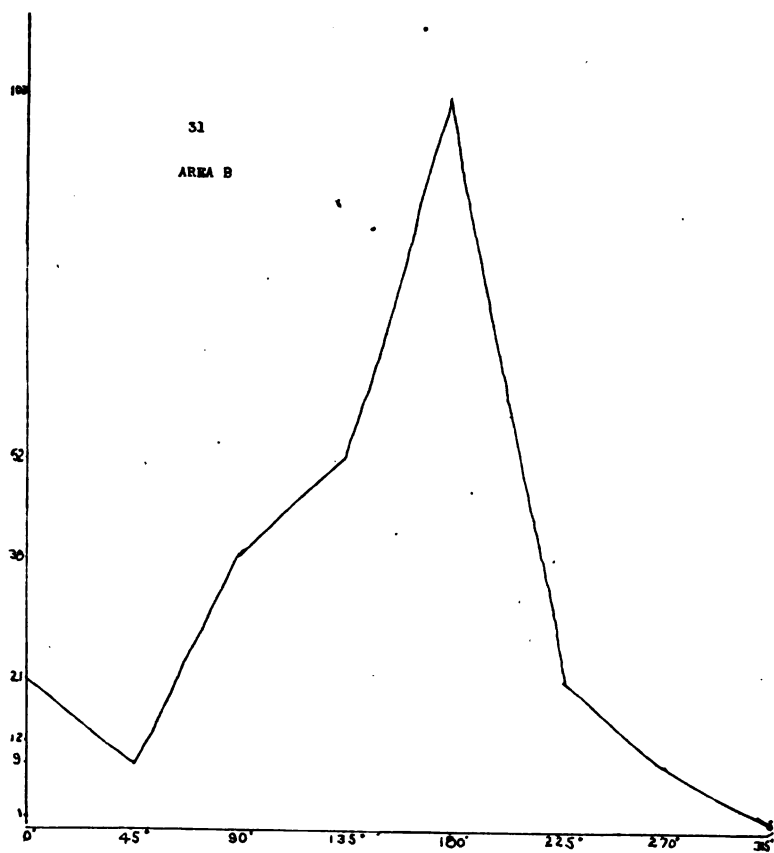
Curve 23, which was constructed from the data furnished by table II and which is a composite curve of all the areas, shows that the normal tendency was to locate the stimulated points below and to the right of their actual position. When we come to consider curves 24, 25, and 26, which are also normal curves for the areas A, B, and C, respectively, we find a very peculiar condition. In area A there are very few cases where the direction of the error was above the stimulated point, the tendency on the part of the subject being to locate the stimulated spot below its actual position. The reverse condition is true of area C. Area B, on the other hand, does not show either of these characteristics. There seems to be almost as great a tendency to locate the stimulated point above as below its actual position. We find this to be true of all the curves.

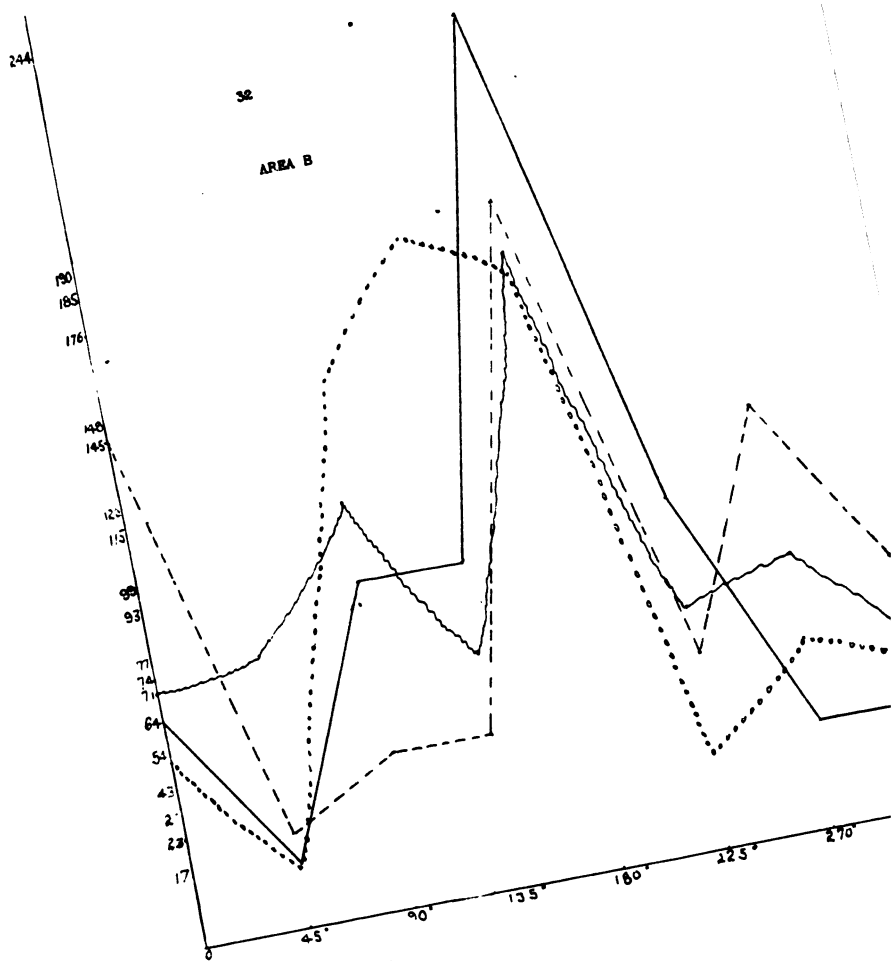
The question immediately arises: what is the cause of this lack of uniformity in the three areas? This is largely, if not entirely, due to the fact that the subject knew beforehand that he would not be touched on any point outside of the square. Consequently, he would never in area A go above the limits of the square, and in area C, below the limits of the square. For example, upon being touched in column 7 of area C and asked to locate the point, he would never place it below the square, even though the stimulus did apparently seem to come from there, he knowing full well that no point below column 7 would be stimulated. The same is true of area A. This probably also accounts, to some extent, for the subject's fineness of localization in area C. If this factor had been excluded, the average error for areas A and C would probably have been slightly greater. This knowledge on the part of the subject acted, therefore, as a disturbing element, and consequently very little can be learned from the study of the curves which show the distribution of the direction of the errors for areas A and C, so that these have been omitted. This, however, by no means invalidates the deductions and inferences made above, since the disturbing element was a constant factor, being present under all the conditions of the problem. The purpose of this problem was not to find out the subject's actual localization power, but, knowing his ability under certain given conditions, to find out what effect a constant stimulus would have upon his ability when these conditions were repeated.

When we compare the various curves representing area B (27, 28, 29, 30, 31) with the normal, or curve 25, we find that in









curve 27 where the constant stimulus was applied to the tip of the middle finger, the number of "ups" ( $0^\circ$ ) has increased to a great extent; in curve 28, where the constant stimulus was applied to the right of the square, the number of "lefts" ( $270^\circ$ ) has increased appreciably; and in curve 30, where the constant stimulus was applied to the left of the square, the number of "rights" ( $90^\circ$ ) has increased to a remarkable degree. In other words, there was a tendency, differing in amount under the different conditions, to pull the stimulated point away from the constant stimulus, that is, to over-compensate for the natural tendency of the constant stimulus to pull the stimulated points toward itself.

This is shown very beautifully in the composite curve 32, which was made by reducing all the experiments on area B to the same total number of cases. Every millimeter on the ordinate is equivalent to two cases. The solid line is the curve of distribution of the direction of the error for the first experiment; the broken line, for the second; the irregular line, for the third, and the circles, for the fifth. Under the conditions of experiment No. 2, the number of "downs" ( $180^\circ$ ) has decreased, while the number of "ups" ( $0^\circ$ ) has increased correspondingly; although the number of "rights" ( $90^\circ$ ), under the conditions of experiment No. 3, has increased slightly, the number of "lefts" ( $270^\circ$ ) has made a tremendous gain; and under the conditions of experiment No. 5, where the constant stimulus was applied to the left of the square, the number of "lefts" ( $270^\circ$ ) is practically the same as in the normal, but the number of "rights" ( $90^\circ$ ) has passed far beyond the normal.

The results of the work embodied in this paper seem to show, first, that the effect of a constant stimulus upon the subject's ability to localize is to increase the amount of the error, and, that in general, the proportion of the increase in the amount of the error is dependent on the nearness of the constant stimulus to the stimulated area; and secondly, that its effect upon the direction of the error is to create a tendency to pull the point stimulated in a direction opposite to that of the constant stimulus, to over-compensate for the influence exerted by the latter in drawing the sensation of the stimulated area toward itself.

















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## **Deficiencies of the Chromosome Theory of Heredity**

**By MICHAEL FREDERIC GUYER, Ph. D.**  
**PROFESSOR OF ZOOLOGY, UNIVERSITY OF CINCINNATI**



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## Deficiencies of the Chromosome Theory of Heredity

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## Deficiencies of the Chromosome Theory of Heredity\*

I should like in the present paper to discuss the evidence upon which inordinate importance has been attributed to the chromosomes as vehicles of heredity, and to inquire into how far this theory agrees or fails to agree with some of the known facts of protoplasmic activity and of heredity. By chromosome theory is meant, in this connection, the original theory which regards the various morphological parts of an adult as specifically predetermined by corresponding anticipatory units which reside in the chromosomes of germ-cells. While many present-day workers, I am aware, do not hold rigidly to this conception, nevertheless, for purposes of criticism it seems best to adhere to a consideration of the theory as expressed and still largely maintained by its founders. To get at the matter satisfactorily it will be best to examine, point by point, the evidence upon which the theory is founded.

1. Roux's ('83) dictum that mitosis is meaningless unless it is for the precise halving of qualities serially arranged, so that, qualitatively, each daughter-cell will resemble the other, is historically, perhaps, the first specification of the chromosomes as centers of series of qualities.

As the case then stood, no evidence had been adduced to show that chromatin is qualitatively differentiated, but theoretical considerations, based chiefly upon the phenomena of what is commonly termed particulate inheritance, had led several biological workers to the assumption that a multitude of particles bearing incipient hereditary qualities must exist in the germ cells. In mitosis was found a mechanism seemingly designed for halving a series of differential particles; consequently, to the chromatin masses which make up the in-

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dividual chromosomes was assigned the rôle of being the actual bearers of the so-called hereditary qualities. As to Roux's avowal that, unless we postulate in the chromosomes discrete qualitative particles which require to be accurately halved, direct division would suffice and mitosis would be superfluous, we know that direct division does sometimes suffice. even for the production of cells which ultimately give rise to germ-cells. In 1894 Meves showed that apparently normal development of spermatozoa may follow amitosis in the salamander. More recently Child ('07) has brought forward what appears to be unmistakable proof of the fact in Cestodes. These cases, of course, neither prove nor disprove the qualitative nature of chromatin, but if chromatin is qualitatively differentiated, the results of these investigators show that the qualities can be distributed without the elaborate structures seen in mitosis, and Roux's argument, therefore, based as it is upon the significance of mitosis, is invalid.

2. The fact that the nucleus is apparently an important center of chemical synthesis has been construed as a proof that it is therefore the vehicle of heredity.

Judging from the results of physiological chemists, it seems probable that the synthetic chemical changes wrought by the nucleus result in part in the construction of incitive or activating materials, in part, presumably, in the further elaboration of nutritive substances; but, to my knowledge, there is no evidence which will warrant us in assuming that the nucleus bears or makes, as it were, self-sufficient morphological units which at just the right time pass out and take up their proper position in the cytoplasm and with the more or less passive cooperation of the latter expand into the structures required.

Everyone will admit, I think, that the cytoplasm of a given species of plant or animal is distinctive of that species in all cells of the organism, and there is no conceivable reason why it, any more than the nucleus, must be made so anew in the germ-cells of each generation. So distinctive of its kind is a given protoplasm, in fact, that there is great probability that in higher animals digested proteids, either in transit through the digestive epithelium or immediately upon entering the blood, are synthesized into a new proteid specifically characteristic of the

animal in which it is present. Here, then, we have a degree of specificity initiated before the proteid in question has ever become cellular in nature.

Of all cells in the body, those which show nuclei of enormous size in proportion to their cytoplasm are not cells which have a large number of morphological structures to establish, but gland-cells characterized by intense secretory activity in which chiefly one kind of product is elaborated.

The death of denucleated, and the regeneration of nucleated, fragments of protozoa are phenomena sometimes cited as demonstrating the fact that the nucleus is the center of morphological synthesis. But may they not indicate only that some general substance elaborated or controlled by the nucleus is wanting? Loeb ('99) has shown that possibly in such cases failure to regenerate may be due largely to a lack of oxygen, and that the nucleus is apparently the chief source of the oxygen supply of the cell. Spitzer ('97) has established the fact, moreover, that certain "oxidation ferments" are nuclear in origin. In these experiments on protozoa the rapidity of regeneration seems to be in direct proportion to the amount of nuclear matter left in the piece—a question of quantity rather than quality. Indeed, if the nucleus is an aggregate of qualitatively different morphological units, one would expect parts to be missing in the regenerated protozoa in proportion to the amount of nuclear matter removed, but the evidence does not bear this out. The regeneration is seemingly complete, only a longer time is required if but a small fragment of the nucleus is left in the piece.

3. Another evidence that is commonly cited may be expressed as follows: Offspring inherit equally from each parent; only one spermatozoon enters the egg normally, and this spermatozoon, though exceedingly smaller than the egg, contributes the same number of chromosomes that are present in the egg. Since only the chromosomes are contributed equally by sperm and egg-cell to the fertilized egg, it is argued that they must be the physical bearers of the equal contributions of qualities from the respective parents.

However, I think we may legitimately question the alleged fact of parental equality in inheritance. While it is true, apparently, that individual or specific characters may be derived

equally from either parent, the fundamental characters that go to make up an organism—such, for example, as make it an animal and a vertebrate of a given family or genus—are characters that are common to both parents; and from a consideration of adult forms alone, therefore, we have no means of definitely determining whether such characters are transmitted by one or by both parent germ-cells. When we come to consider embryological stages, however, the evidence at our command, meager though it be, plainly indicates that we do not inherit equally from each, but more from the maternal parent.

Since I have discussed this matter at some length in a former paper (Guyer, '07), I shall cite but a single instance in this connection. Both Conklin ('05) and Lillie ('06), if I do not misinterpret their results, find that in certain forms, before the spermatozoon enters, the fundamental organology is already roughly indicated in the egg by the distribution of so-called "formative substances." The egg then passes on to cleavage without waiting for a duplicate set of "formative substances" to pass out from the male pronucleus. Since there is evidently no biparental mechanism present in these early and more fundamental stages, we are not justified in maintaining that offspring inherit equally from each parent. Consequently, if we insist on restricting *all* of the mechanism of heredity to the chromosomes, the argument from the striking parity between the chromosomes of male and female germ-cells loses its force.

It is true that in these cases cleavage is not inaugurated until the spermatozoon enters the egg, but here we must discriminate between simply the stimulating effect of the sperm and its capacity for conveying hereditary qualities. That this is a valid distinction is evidenced by the facts of artificial parthenogenesis, where by various artificial means the mere stimulus to cleavage may be brought about.

It may be urged that although "organ-forming substances" are present in the cytoplasm of certain eggs before fertilization, these substances have originated from the nucleus during the earlier history of the egg-cell. There is good evidence, in fact, to show that the cytoplasm of the egg is more homogeneous in appearance in earlier stages than later, and that substances are ejected into it from the nucleus. However, this does not prove

that these nuclear emanations are morphological entities, and I see no sufficient reason for not regarding them simply as nuclear products which cooperate with cytoplasmic substance of equal importance in the construction of materials which may serve as a basis for further differentiation. In any event, the disparity between maternal and paternal inheritance would remain.

Inasmuch as the bulk of the egg, even after fertilization, is cytoplasm chiefly of maternal origin, it is clear that the developing organism is more maternal than paternal in its derivation. Nevertheless, we can see how the veneer of individual traits may be equally of maternal and paternal origin if, to express it crudely, we look upon cytoplasm and chromatin respectively as responsive mechanism and inciting agent—the character of the response depending upon both the constitution of the cytoplasm and the materials (enzymes? nutritive substances?) emanating from the nucleus—subject, of course, to the restrictive influences of the environment. We know, furthermore, that individual parental characteristics appear for the most part as modifications of characters held in common, rather than in the presence or absence of special characters.

So it seems not improbable that, as the proper stages in development are reached, the secretions or emanations from the chromosomes of paternal and maternal origin can produce in combination or interaction with the cytoplasm and the general environment the ultimate characters peculiar to the respective parents. From what we already know of physiological chemistry we can but conclude that before the final adult organism is evolved there must ensue numerous reactions between the nuclear material and the cytoplasm, and probably many highly complex interactions would follow, both among the products of these reactions and between them and other nuclear and cytoplasmic materials which had been developed in the meantime, or which had remained quiescent because of the want of proper material with which to react.

By way of rough analogy, the writer has always thought of the process of specific organogeny as possibly somewhat similar to the production of galls on plants. Any one of several species of insects may produce galls on a given plant, but each kind of insect always produces its own specific type of gall. Here is an actual case of living protoplasm producing a specific character

through the activity of a specific exciting agent. That is, the reaction between certain secretions of the insect and the living substance of the plant produces new and definite structures. Change either factor and the resulting structure must be modified.

Likewise, in the germ-cell, alterations in the constitution of either chromosomes or cytoplasm must undoubtedly produce structural changes in the adult. It would seem that one might expect to find in the chromosomes the greater source of variability because they are derived in much greater proportions from two sources—the two parents—than is the cytoplasm, and this very mingling of the two materials could afford an adequate basis of both quantitative and qualitative changes. The changeable nature of chromosomes is evidenced, furthermore, by their marked differences in structure and appearance under different conditions of activity, and their instability is shown in the pronounced irregularities which may arise through hybridizing or from such external influence as drugging, etc.

In so far as the cytoplasmic constitution is altered before the germ-cells are specifically set aside, we might reasonably expect this constitution to persist as such in the cytoplasm of these cells. We can readily see, moreover, if persistence of such a cytoplasmic constitution is possible, how changes of chromosomal constitution (or, indirectly, even the effects of physical environment) might be reflected onto the cytoplasm from time to time, and there conserved.

A pursuit of this line of thought is tempting, but it would lead us far astray from our subject-matter. Nevertheless, it is well to remember that from the very fact that racial evolution is possible we must concede an accumulative capacity of some kind to the germ-cell. However our respective judgments may balance the factors of preformation or epigenesis in ontogeny, the fact confronts us that phylogenetic development has been largely an epigenesis, since in the first living matter there could not have been specific organ-forming substances for all the later organisms which have evolved from it. If organ-forming substances are necessary for the ontogeny of present forms, it is a necessity which has been acquired hand in hand with the evolution of the race, and the problem which confronts us is to solve the riddle of how it has been cumulatively grafted onto the pristine protoplasm.



4. The presumed necessity of a reduction in the number of qualities which arise as the result of dual ancestry, together with the fact that there are reduction divisions strikingly similar in appearance and results in the germ-cells of both male and female, is also regarded as a proof that the chromosomes are the bearers of the hereditary characters. As a consequence of these reduction divisions, the male and female germ-cells each come to have only half the number of chromosomes characteristic of the ordinary tissue-cells, a fact which is interpreted by Weismann and his school as indicating that half the hereditary qualities have been eliminated in each germ-cell. The total number of chromosomes is restored again through the act of fertilization.

Even ignoring the fact that reduction divisions of chromosomes do not occur in a number of seemingly well-authenticated cases, the theoretical necessity for qualitative reduction is by no means obvious. In the first place, it is improbable that the number of qualities are doubled at conjugation because, for the most part, leaving out of consideration superficial individual differences, probably like protoplasm is added to like protoplasm; or possibly, as already suggested, the male brings in materials which can participate in the construction of a more limited number of characters. As to the difficulty regarding the ultimate accumulation of individual qualities, there is evidence that they may often blend in time, or that certain ones become dominant. Finally, as far as probability is concerned, it is just as likely that inactive qualities, if represented materially, might be resorbed by the protoplasm (just as we have resorption of visible morphological structures, such as the tail of the tadpole) as that a complicated mechanism for throwing out half the qualities of each germ-cell is necessary.

Weismann himself has shown, in fact, how, according to his theory of heredity, through panmixia (cessation of natural selection) and the battling of "determinants" for nutriment, a useless part "must grow smaller and smaller until finally it disappears altogether." (*Germinal Selection*; second edition, p. 42.) If one accepts this view of the elimination of superfluous qualities, it is difficult to see the necessity of postulating a second method of elimination by reduction divisions, or how, indeed, in the course of evolution the enormous supply of accessory or

reserve characters which are attributed to the germ-plasm, could have arisen.

5. The perpetuation through successive cell-generations of a fixed number of chromosomes, each apparently of distinct individuality, together with their final seeming accordance with the idea of "pure" germ-cells as demanded by Mendelian principles, is regarded by many as one of the strongest supports of the chromosome theory of heredity.

That there is at least a kind of individuality (recurrence of form) of the chromosome is clearly demonstrated in the results of such investigators as Herla ('93), Zoja ('95), or Moenkhaus ('04), who have studied the chromosomes of hybrids from widely separated forms which have noticeably different chromosomes. And the same thing is shown almost as conclusively, I think, in the researches of Montgomery ('01), Sutton ('02), Wilson ('06), and others who, working upon non-hybrid forms which have chromosomes of varying size, have accumulated much evidence to the effect that in somatic and early germ-cells pairs of homologous chromosomes exist, one member of each pair being maternal, the other paternal, in origin. Persistency of form, however, does not necessarily imply persistency of constitution. This is evident when we consider that a chromosome is a complex made up of at least two substances, viz., an apparently more homogeneous linin substratum, encasing innumerable granules of chromatin. Whether any exchange of individual granules occurs, or whether any permanent changes are wrought in the chemical constitution of these granules or of the surrounding cytoplasm, we have at present no direct means of ascertaining. It is certain that abundant opportunity for such alterations is afforded when chromosomes are resolved into their ordinary diffuse condition in the nucleus.

Granted that in hybrid offspring there are such things as germ-cells "pure" with respect to a given character—and there are some who would dispute this—it would seem, if we assume that the chromosomes determine certain hereditary characters, that in the separation of homologous chromosomes of different parentage an adequate mechanism exists for the segregation of these qualities, as has recently been advocated by various cytologists. Doubt is cast upon this interpretation, however,

by such facts of non-Mendelian inheritance as blending, the persistence of hybrid mosaics, and the lingering of certain influences in gametes which theoretically should have been purged of such characters.

The very fact, however, that constant types of visibly different chromosomes recur time after time in cell divisions shows, at least, that under certain conditions they possess different physical properties, and that in some respects, therefore, they are qualitatively different. But there are no sufficient reasons, I think, why we may not look upon their differences as differences of more elemental chemical and physical constitution rather than as differences among systems of determinate morphological units. Because when the two are brought together under certain conditions water ( $H_2O$ ) is the result, we do not postulate a "determinant" of "aquosity" in hydrogen or in oxygen. It is true that in view of certain properties possessed by each of the two gases, the formation of water is possible, but bring them together under other conditions and the same two elements yield an entirely different "character," viz., hydrogen peroxide ( $H_2O_2$ ). Or, again, let chlorine act upon benzene ( $C_6H_6$ ) and, depending upon purely quantitative relations and other physical conditions, any one of six different substitution products ranging from  $C_6H_5Cl$  to  $C_6Cl_6$  can be secured. No quasi-teleological conception of anticipatory units is found necessary in a consideration of such cases of chemical configuration, and it seems to me that its necessity, as implied in the conception of determinants or pangenes, is yet to be demonstrated in phenomena of heredity. Even in case of the divorcement of paired parental chromosomes in gametes—and I think this is strongly evidenced in a number of Tracheata—it would seem that we might account for the so-called Mendelian phenomena by attributing to the chromosomes simply chemical and physical differences without endowing them with morphological entities. And, moreover, on such a basis, looking to the reactions of nucleus and cytoplasmic materials for the establishment of ultimate "characters," we can more readily see how non-Mendelian gradations and "contaminations" of characters might arise, because we might then attribute more importance to purely quantitative relations and chance mixture of the chemical substances. In short, there can be a "qualitative" basis, or a series of qualitative bases, without these

being at the same time specific "determinants," and until such a more neutral qualitative basis for the phenomena of heredity is shown to be untenable there is no valid reason for postulating a series of morphogenic entities.

But such considerations as these open up another important question, viz., as to just how we are to regard heritable qualities. One great difficulty here lies in the vagueness which enshrouds the term "quality" or "character." It is obvious that many so-called characters are in reality only the expression of the relations of a number of parts and can have no individual basis of their own.

In all our systematic zoology *stability* is the fundamental principle used in selecting characters for purposes of classification. For example, the features chosen as characteristic of genera have shown themselves to be more constant than those which are selected to indicate species, otherwise they would have been discarded as generic characters; specific characters, in turn, are less fluctuating than varietal traits. The qualities which stamp a given animal as a vertebrate or a mammal are certainly more stable and definitely coordinated than those which mark it as a particular variety or species. Our whole scheme of natural classification, which is, when correct, but an expression of the evolutionary status of the forms classified, is based necessarily upon the facts of heredity—that is, of community of descent. Does not the very fact itself that certain character relations are uniform and others fluctuating through successive generations show that in seeking for a physical-unit basis of inheritance we cannot expect to find it wholly in a series of equipotent units, but that unmistakably we have to deal with groupings of characters, some groups of which are more stable than others? This, in turn, can mean only that any such group must be a unit in itself, and that we are dealing, therefore, with units of a higher and of a lower order; or, in other words, with series of coordinations built upon broader coordinations.

To some, such an admission may seem inevitably to demand as a consequence some kind of morphological basis or organization in the germ-cell, some coordinating influence, to which the more restricted chemical processes are subordinated. However this may be, it assuredly does not make an accompanying demand that such controlling factor or factors shall reside wholly

or predominantly in the chromosomes. The so-called "organism" standpoint, indeed, which as new facts come to light is appealing to more and more minds, would seem to tend rather toward conclusions just the reverse of this or of any that would seek to localize the adult morphology of a living organism in any special part of its antecedent germ-cell. A germ-cell, in fact, should need no special units to generate the peculiar *genre* equilibrium or idiosyncrasy of protoplasm which is distinctive of a particular kind of individual, since such a germ-cell not only is itself already an individual, but from the very fact of having had the same racial history as other individuals of its peculiar kind (be they germ-cell, embryo, or adult) it must likewise as a whole already possess this distinctive idiosyncrasy.

The results of recent experiments on regeneration and regulation tend, in so far as they have bearing on ultimate organogeny, to emphasize the significance of an organism as a whole to its environment, together with its physiological coordination or interaction of parts. The results of such work seem to indicate clearly, as ably maintained by Child ('06), a fundamental physiological unity of the entire organism to account for which any purely "unit-character" basis of transmission is inadequate.

To express the phenomena of organic characters, it would seem that we must turn to a condition somewhat analogous to that with which we meet in chemistry in many organic compounds; and while the comparison is only an analogy, we might well remember that it is an analogy drawn from organic matter itself. For example, in many organic compounds we have certain fundamental groups of comparatively great stability, well illustrated in the so-called benzene ring. We can substitute for the hydrogens of this ring one, two, or many alkyl or other groups, thus producing different compounds. Yet these compounds have certain fundamental properties in common, due to the benzene ring.

While in living beings qualities must be looked upon as more or less flexible rather than absolutely static, with certain possibilities of blending, of gradational and of cumulative effects, still we must recognize more and less stable coordinations. But even in this matter of flexibility chemical and physical analogy does not forsake us, for we find many analogous examples of similar flexible or gradational combinations, in which the

components may establish any proportional relation one to another, depending upon external factors. This is best evidenced in solutions, and especially in certain solid solutions. Moreover, in phenomena of "dynamic isomerism," in changing substances of the same chemical composition but of different structure one into another, we can get a condition of equilibrium between the two at any point, the condition of this equilibrium depending upon temperature, pressure, and concentration. Again, in allotropic forms of such substances as sulphur, phosphorus, tin, etc., various conditions of stability can be brought about in different ways.

6. Boveri's demonstration ('89, '95), that the denucleated egg of one species of sea urchin when fertilized with the spermatozoon of another species shows purely paternal characters, has been numbered among the proofs of the exclusive control by the nucleus of matters of heredity.

Both Seeliger ('95, '96) and Morgan ('95), however, have shown that even when the egg is not denucleated, still, in hybrids between the forms with which Boveri worked, the paternal type may occasionally predominate, to the apparent exclusion of the maternal type; that, in fact, Boveri's experiments may mean simply that in such cross fertilization the characters of the male species are prepotent over those of the female species. Furthermore, as just the converse of Boveri's results, we have Godlewski's ('05) observations that non-nucleated pieces of sea-urchin eggs, fertilized by sperm from a crinoid, produced larvae *exclusively of the maternal type*.

7. The apparent association of specific qualities of the adult with specific chromosomes is regarded as another support of the chromosome theory of heredity. The most noted example of this is the finding of a chromosome that is regarded as a possible sex determinant in certain tracheata.

We cannot enter here into a review of this intricate matter, a detailed discussion of which will be found in Professor Wilson's ('06) paper. While the whole question of whether sex is pre-determined, or whether it may be determined after development has begun, remains almost as much of a puzzle as ever; still, if there is any truth in the latter alternative, the trend of ex-

periment points mainly to the conclusion that nutrition is the chief factor in determining sex. Consequently, since of the insects exhibiting the "accessory chromosome" the females are characterized by the presence of an extra chromosome (or by a greater bulk of active chromatin in case idiochromosomes are present), we seem justified in asking that it be shown untenable that the production of females is due, not necessarily to special sex-determinants in the chromosome, but to the presence of more chromatin which has meant increased chemical activity on the part of the nucleus. In the few cases where the idiochromosomes are of equal size, however, purely quantitative relations are apparently inadequate as an explanation. But even here there may be a difference in intensity of chemical activity between the two chromosomes, since, in this group of insects, according to Wilson, there are indications of a tendency of one of the idiochromosomes to disappear ultimately.

The observations of Boveri ('02) on echinoid eggs which have been fertilized by two spermatozoa is also regarded by some as strong evidence that the nucleus is the real bearer of hereditary qualities. We must recognize, however, that in such cases as the production of three cells by means of a tri-polar spindle, for example, the cytoplasm of the sperm, scant as it may be, is also distributed among the three cells, as is also the substance of the spindles; so that the result is not three different series and combinations of chromosomes in three cells of similar protoplasm, but a series of chromosomes in cytoplasm, which itself differs in the three cells. Again, if the individual chromosomes differ only in that they produce different nutritive materials, or enzymes, then we might expect different and abnormal results from different blastomeres, since the cytoplasmic mechanism could only react on or be stimulated by the substances distributed to it. Thus absence of parts in a portion of the body developed from a blastomere in which an insufficient number of chromosomes is present might well be expected, and the whole phenomenon is as easily interpreted to mean that, considering nucleus and cytoplasm as of coordinate importance in inheritance, a proper reaction has been prevented or that insufficient material was present. as to regard it as a demonstration of the exclusive importance of the nucleus in heredity.

Lastly, inconstancy in the number of chromosomes in closely

allied forms argues against the idea that we shall ultimately be able to associate specific characters of the adult with individual chromosomes. The numerical differences would seem to be out of all proportion to the actual differences between the adults of the species or genera showing such discrepancies.

On the other hand, if we find closely allied genera or species with chromosomes very constant in number and appearance, even should they have no causal connection with the phenomena of heredity, one need be no more surprised than at finding close similarity among any other organs in closely related species. It might be argued, indeed, with some plausibility, that the number and arrangement of the chromosomes in a given species are the effects of the fundamental constitution of a given kind of living matter, rather than that they stand in a specifically casual relation to such constitution.

By way of final summary with regard to the proposition that the chromosomes are the exclusive vehicles of heredity, we may, I think, deny that a satisfactory case has as yet been proven. While the jumble of facts which have been determined so far may not negate the theory, still we are not justified for that reason in maintaining that they substantiate it, especially when most of the facts are so Janus-faced as to be of equal utility in confirming other hypotheses.

The important fact always confronts us that a given kind of protoplasm is a protoplasm peculiar to the organism of which it forms a part, whether the latter be amoeba or man, and the egg as a whole, both cytoplasm and nucleus, therefore, has its own individuality. Hence no special formative force has to change it into a specific kind of protoplasm before the more obvious morphological entities can become manifest. Heredity is a problem of the handing on of metabolic energies already established, rather than of the transmission of a series of determinative units which create a wholly new organism. We can see that in so far as the substances constructed by the nucleus are peculiar or individual, the number of structures the cytoplasm can shape from such material or form in combination with it has been restricted, and in this sense the nucleus has conditioned heredity. But because the three elements, carbon, oxygen, and hydrogen, condition substances of which they are components, we do not



postulate a specifically determinative substance in any of them for each of the numerous carbohydrates and carbohydrate products that result from their various combinations and arrangements. What the chemist seeks to determine are the quantitative and other physical relations necessary to the establishment of a certain molecular configuration. Likewise, what we seek in heredity are the shaping and controlling factors which bring materials into place that they may combine in the proper way and at the proper time. This much is certain: no chemical, physiological, or morphological evidence is yet extant which places these factors wholly within the chromosomes.

I do not desire to minimize the importance of the chromosomes in heredity, and I think no one would deny that they may stand in definite causal relationship to adult characters. On the other hand, I see no sufficient reasons for denying that other germ-cell constituents may, in the same sense, stand in causal relationship to such characters. In these initial substances, however, I see no more necessity for postulating specific anticipatory characters (beyond the properties which makes a given substance a substance *per se*, irrespective of the structures into which it may ultimately be builded) than I do of regarding yeast, or flour, or milk as in itself a specific determinant of a loaf of bread. While the net results may be in large measure the same, whether we accept the rigid "determinant" idea or whether we adhere to a more neutral qualitative basis, there are certain elements of freedom in the latter conception, I think, which render it a safer foundation for unbiased investigation of the problems of heredity. I would plead, therefore, not for the abandonment but for the maintenance of other working hypotheses as our greatest safeguard.

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## Studies on Phagocata Gracilis (Leidy)

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## PHAGOCATA GRACILIS (Leidy)

In connection with certain problems in Phagocata, upon which I am at work, there have come to light many interesting facts concerning the life history and morphology of the animal, and it is the object of this paper to treat upon these points. The anatomy of the various Planariidae is essentially similar and has been fairly well worked out for the different species by various investigators, to some of whom I shall have occasion to refer. I have found Dr. Woodworth's paper on *Phagocata gracilis* of great value and interest, but, on account of several important points of conflict between his work and mine, I find it necessary to cover again a considerable amount of the ground over which he has already gone.

I have also received much valuable information concerning the habits and characteristics of Turbellaria, as well as much assistance in interpreting the problems presented by my slides, from Professor M. F. Guyer and Associate Professor H. M. Benedict, of the University of Cincinnati, to whom I wish to extend my most sincere thanks.

Phagocatae are not infrequent in fresh water in various parts of the world. Running streams seem to be their most frequent habitat, but they are found as well in ponds and lakes. They will be observed gliding along the beds of shallow streams, or, as is mostly the case, under stones or leaves which are beneath the surface of the water. At times they may be found in thousands crawling along the sandy bottom of a brook as if migrating.

*Phagocata gracilis* (Plate I, Fig. 1) is a small, bilaterally symmetrical flatworm, ranging in size from four mm. long and one wide, to thirty mm. long and six wide. The margins of the body are elongated and somewhat parallel, converging a little at the anterior end to mark off the head region, and taper-

ing markedly to a point at the tail end. The body is flattened dorso-ventrally, being flat or even concave on the ventral surface, while the dorsal side is arched to a slight extent. When at rest Phagocatae appear quite varied in form (Plate II, Fig. 17 B). Some individuals retain the above mentioned shape; some become very irregular in outline; others spread out until they are as wide as they are long; while still others curl up into complete balls. In fact no definite rule can be laid down as to how they will appear when quiet, yet ordinarily they will be short, thick, and wide, with wavy edges. It is a common thing to see Phagocatae resting not singly, but in groups of considerable number. They seem to collect on the sides of the aquaria or in a heavy scum of bacteria at the farthest possible distance from the direct light, and will, apparently, often remain there for days.

The *reaction to light* in the case of Planaria and Phagocata is probably not to be considered heliotropic. Almost every action of uneasiness which they show when exposed to strong light is greatly increased when the exposure is sudden. In such a case they apparently seek more mollifying conditions, and thus will collect in the darker parts of the aquarium. They do so, however, not in the direct course laid down by heliotropism (Loeb '06, Chap. VII), but by the same roundabout, zig-zag course which they employ at all other times. Moreover, the place of minimal intensity of light is in many cases (round aquaria) at the sides, and not directly opposite the entrance of the light rays; and several investigators have noted that Planarians more often congregate in these positions than elsewhere. Though frequenting the darker parts of the aquarium for the most part, Planarians are evidently not forced by any reaction to light to remain there, because they are not infrequently found swimming about over the brighter parts.

Loeb ('06, p. 136) has observed these same facts, and in summing them up has distinguished between his general theory of Tropisms and this apparent reaction (*unterschieds-empfindlichkeit*) to direct or intense light, as follows: "There are other forms which react as well upon sudden increase as upon a sudden decrease of the intensity of light, e. g. fresh-water Planarians and earthworms. In these forms a sudden increase in the intensity of the light causes restlessness, while the reverse change causes the animals to come to rest. This may lead to

the gathering of the animals in such parts of the vessel as represent relative minima in the intensity of illumination. When such an animal comes from a bright spot to a darker spot it comes to rest ('falls asleep'). In consequence of this fact such a relative minimum must act like a trap in which the animals are caught. The consequence is that the number of animals collecting in such a place must always increase, inasmuch as any animal which gets to such a spot by chance must remain there because its motions cease."

One can perceive how it is quite possible for the animals to be effected by light, and under too irritating conditions to seek darker places, but it is as hard to see how this purely mechanical explanation of Loeb can force the worms to seek the place of minimal intensity of light by the roundabout course which they pursue, as it is to understand how Pearl's ('03, p. 619) "delicately balanced and finely co-ordinated reactions of the organism as a whole" can bring about the same result. We must admit that intensity of light causes uneasiness, and therefore movement which can be conceived of as a "trial and error" attempt to escape the disagreeable conditions. Still we cannot overlook the fact that these movements, however irregular they may be, are the results of certain body systems which are on the whole definitely coordinated, and therefore responsible to a certain degree for the body actions. For this reason it appears that neither the absolutely mechanical nor the definitely coordinated system can, in itself, produce the ultimate moving away from the intense light to darker places and collecting there; and so we are forced to admit that there must be present either other conditions, or some combination of these two.

*Coloration* varies quite extensively, the young being usually lighter than the older ones. The majority of fullgrown *Phagocatae* taken fresh from the stream appear almost entirely black. Frequently, however, one may be found which is distinctly brown in color, and once in a great while a pure white or cream-colored one may be discovered. The ventral surface is never as deeply colored as the dorsal side, and in the black specimens it appears a little greenish, while in the brown ones it is of a lighter color than the upper surface. After remaining in the aquarium for some time, scarcity of food and change of environment seem to moderate the density of the color, and they

appear somewhat of a dull greenish black in the majority of cases. The presence of a distinctly colored food in the alimentary tract is often misleading in determining the actual color of the animal, unless one is well acquainted with its food habits (page 19 on digestion). While crawling on the sides of a glass aquarium and viewed against the light, it appears quite translucent, and usually of a brown color. When in this position many of the internal organs are plainly visible (Plate II, Fig. 17a).

The *pigment* is, in general, in the form of minute granules varying in color from brown to green and even black, and is located in irregular patches underneath the epidermis and between the muscle bundles. In many specimens, usually the oldest ones, rhabditi (see page 9) may be found in profuse number scattered so densely throughout the epidermis as to practically replace it. These rods are larger than those found in the younger specimens, and are often of such a dark color that they determine the coloration of the animal.

The body is divided into two distinct regions, namely, the head and trunk. The *head* occupies only a small portion of the whole length of the body, at the most not over a fifteenth. In the extended condition it is approximately straight across the front, and is not as wide as the trunk region. The outer corners sometimes protrude and give the appearance of ears, as is common in *Planaria maculata*, but in general this is not the case. There are two eyes, which one may see by careful observation without the aid of a lens.

The *trunk*, occupying the remainder of the body, is flexible and non-segmented. It shows very little differentiation to the naked eye except that its sides are somewhat parallel, tapering to a point at the tail, and that a blackish median line is often present down the center of the dorsal surface.

In section the trunk varies in structure according to the location of the cut, but any section will give the general structure. The outer surface is formed of *epidermal cells* which are of the columnar type, but are usually much distorted. The cells of the dorsal surface are as much as twice or three times as long as they are wide and contain large nuclei situated near the base. The presence of the great number of rhabditi between these cells, however, often disfigures them until they appear of numerous shapes, being commonly somewhat fungi-



form, and in this condition the nuclei may be forced to almost any part of the cell (Plate I, Fig. 2, d.ep.). Woodworth finds that the dorsal epithelial cells show a striated appearance, but I have not been able to distinguish this characteristic with any certainty. I have found a few cells which appeared to have striations, but they were in thick sections, and I am inclined to attribute their presence to other causes. The *rhabditi* are peculiar rod-like structures which are secreted by parent cells located in the parenchyma (Plate I, Fig. 2, rh.c.; and Fig. 8, rh.). Several functions have been attributed to them by different authorities. Some claim they are physiologically equivalent to the nematocysts of the Coelenterates, while others think they are similar to glandular secretions. According to Woodworth ('91, p. 20), "The dermal rods are to be considered as condensed secretions arising in sub-hypodermal unicellular glands of ectodermic origin. The rhabditi are being continually cast out of the body and replaced by new ones developed in new parent cells within the body of the parenchyma. The connection of the parent cells with the epidermis is a primitive one, and the rods pass to the exterior by means of the tubular ducts formed by the neck of the elongated cells. The rods lie between the cells of the epidermis; they are slowly soluble in water, and are used by the animal in securing food and for protection."

On the ventral surface the epidermal cells are much more regular than on the dorsal side. They are practically cubical, and the nuclei are arranged regularly near the bases. Rhabditi may be present here in the case of the older specimens, as was mentioned under coloration, but they are fewer in number and are usually perpendicular to the body wall in general. Covering the outer surface of these cells and also those upon the lateral edges of the body, are numerous *cilia*. They are somewhat longer near the edges, and especially so about the mouth and head regions (Plate I, Fig. 2, cil.).

Directly below the epidermal cells is the *basement membrane* (Plate I, Fig. 2, b. m.). In the great majority of cases this membrane is invisible because it does not take stains readily, but commonly its presence can be determined by the clear space between the epidermis and the muscular layer below. Under very high magnification the membrane appears as a clear homogeneous band of tissue of a slight grayish color which, in most cases, is closely attached to the circular muscle layer

below it, but occasionally may be found adhering to the epithelial cells when they have been torn away from the underlying tissue.

The *musculature* of *Phagocata gracilis* consists of three distinct systems: the circular, longitudinal, and dorso-ventral. The *circular muscles* form a somewhat narrow band of fibers lying directly below the basement membrane to which, as mentioned above, they closely adhere. The juncture formed by the membrane and the circular layer presents practically a straight line, and in no place can I find the circular muscles indenting into the basement membrane as Woodworth has stated. The function of this layer is mainly to elongate the body by contraction of its fibers (Plate I, Fig. 2, d. c. m., v. c. m.).

The *longitudinal muscle band* which rests in contact with the inner surface of the circular layer varies at different parts of the body. In general it consists of large bundles of fibers which project irregularly out into the mesenchyme and also indent the circular band. High power magnification shows that these bundles are further divided into smaller feather-like groups of fibers which in many cases have clearly marked outlines. In general the bundles are irregular in form and appear to connect with the circular layer only at places, thus leaving clear spaces scattered along between them. Within these clear spaces, between the bundles of longitudinal fibers and along their surfaces, and also upon the inner side of the circular muscles, may be found many large nucleated cells and numerous pigment granules. The chief function of the longitudinal muscles is to shorten the length of the body and to bend the extremities upward or downward by contraction of dorsal or ventral bundles respectively (Plate I, Fig. 2, d. l. m., v. l. m.).

The *dorso-ventral muscles* which form the third and last system are found only in scattered bundles. They traverse the mesenchyme from dorsal to ventral surface and attach either to the inward projections of the longitudinal bundles, or, passing between them, connect with the inner surface of the circular layer. Their function is to narrow the body dorso-ventrally (Plate I, Fig. 2, d. v. m.).

The *mesenchymatous tissue* which makes up the bulk of the body is varied in structure. In the younger specimens it is composed to a great extent of large somatic cells of irregular form, each having a well defined nucleus. Somewhat later msto

of these cells seem to break up and form the irregular mesh-work of fibers with scattered nuclei, which is most commonly found in sections (Plate I, Fig. 2, mes.). Throughout the entire extent of this tissue irregular cells and cell spaces interlace with the above mentioned fibers. A very distinct series of open spaces seems to be arranged along the dorsal and ventral parts of the so-called "pseudocoel" directly within the longitudinal muscle layer (Plate I, Fig. 2, 3-5, 14-16, s. m. s.). They compose to a great extent the spaces between the projecting bundles of this layer, and are much larger on the dorsal side where the bundles are more conspicuous. In old specimens the rhabditi are found in numerous masses throughout the epidermis and also fill these spaces.

Spermaries which are filled with developing spermatozoa are also scattered throughout this mesenchymatous tissue; they will be discussed later. Yolk glands or at least similar appearing structures may be found at certain seasons. The dorso-ventral muscle fibers may be seen running along in scattered bundles in almost any part of it. Large cells which appear to be the maternal cells of the rhabditi mentioned above are also common. They are mostly globular or somewhat flask-shaped, and in some sections the opening duct may be observed passing upward through the superimposed network of tissue, penetrating the muscular layers, and finally opening to the exterior between the epidermal cells (Plate I, Fig. 2, rh.c.).

Woodworth ('91) has found two systems of *glands* which open to the outside, and my slides show similar structures. One of these systems is located near the genital pore and the other in the head region. The latter arises as two tubes slightly in front of the ovaries. These tubes pass above the brain, and, turning downward, open on the ventral surface close to the anterior end. They are irregular in form, and have numerous swellings in each of which is located a dark-staining homogeneous nodule of tissue. The functions of these two systems are unknown.

The histology of the remaining organs will be considered under separate headings.

Returning again to external conditions, it will be well to consider here the thick, sticky fluid, very disagreeable to the taste, which is secreted by the ectoderm. Under normal conditions this mucus seems to aid the body in moving, and proba-

bly serves for protection and as a method of capturing food as well. When sudden changes in temperature occur, or when the animals are left for some time without food and change of water, this fluid secretion becomes very noticeable. If Phagocatae are placed in a vial, the water soon becomes filled with a fine meshwork of almost colorless threads in and out amongst which they glide at will. When an aquarium is subjected to the abnormal conditions just mentioned, and also often when no apparent change of conditions has taken place, the animals will congregate either individually or in groups upon the under side of the thick bacterial scum at the surface of the water, and, slowly wending backward and forward, secrete a profuse amount of mucus. This, mingling with the scum on the water and the particles of mud gathered in it, soon hardens and forms an effective protection for the individual or individuals within (Plate II, Fig. 20-21).

I had always considered this a method of protection against environmental changes, but it was not until lately that I was able to obtain definite results which prove the case. Specimens going into cysts while in the aquaria were watched, and without exception were found to remain in the same condition for a long period and finally, after several months (often five or six), to gradually decompose and disintegrate. If, however, the cysts were enclosed in very fine wired cages and replaced in the brook from which they had previously been taken, the Phagocatae soon emerged and were apparently in as good condition as when formerly in the stream, except that they were somewhat smaller. The animals make their exit from such cysts by working out through the walls, which are apparently quite penetrable. It is not clear whether or not the openings made in this way remain, but it is certain that the animals often reenter the original jelly-like cyst and become dormant again if the conditions become unfavorable. The name "protective encystment" has been applied to this peculiar characteristic of flatworms.

The power of *locomotion* in Phagocata is fairly well developed considering its low position in the animal kingdom. We find in general two kinds of movement, a smooth gliding motion, and a crawling movement. The first or gliding motion is brought about by the numerous cilia found on the ventral epidermis. In life these may be observed, by careful

manipulation of the microscope, rapidly beating back and forth all along the ventral surface and the lateral edges of the animal. Across the front of the head and upon the lobes the cilia appear to be much longer and move more slowly, beating from the center toward the lobes and backward toward the tail. Woodworth ('91) records finding cilia all over the whole body surface, but my sections show the cilia only upon the ventral and lateral ectodermal cells; they are missing from the dorsal cells. Bardeen ('02) finds a condition similar to this in *Planaria maculata*, and states that cilia are never found on the dorsal surface. This fact coincides well with the animal's method of movement, in that the secretion in which the cilia beat is given off more profusely from the ventral body wall, and, moreover, the animal glides with its ventral surface against either some solid object or the surface film of the surrounding water. For this reason it is hard to see how cilia on the dorsal surface could be of much aid in the case of movement.

The crawling or looping movement is due entirely to muscular contraction. When upon solid surfaces Phagocatae will often move in this way, especially if there is a scarcity of water or if the current is quite swift. Through a curving-in of the ventral surface of the body, either as a whole or in local areas, suction is effected, and the body is thus held firmly to the surface with which it is in contact. This suction device is used in making the characteristic looping "inch-worm" movement of locomotion, and likewise apparently as a means of holding the animal's body in contact with the under side of the surface film of the water, either when swimming there or when at rest. When disturbed a series of writhing movements occur which are caused by the alternate contraction and expansion of the various muscle systems.

The *mucus secretion* of the ectoderm, mentioned above, seems to be to a considerable extent an aid in locomotion. It is very sticky in nature and adheres immediately to anything with which it comes in contact in the water. The cilia beat rapidly in this medium and inasmuch as it remains stationary, the body is moved forward. A whitish streak of mucus is often seen in the wake of the moving worm. If, when swimming on the surface, it is suddenly dislodged, it will cling by its tail to the surface, or if it is not able to do this it will hang by a slender thread of mucus and slowly sink to the bottom. When several

specimens are placed in a small vial, as mentioned above, they will in a short time have the water entirely filled with interwoven mucus fibers, which, in time, sink and form large masses of slimy material.

The *bodily activity* in all Phagocatae is somewhat periodical. At times during the day they will be seen moving energetically about, and again one may find them grouped and apparently at rest. During the night they appear to be almost constantly in motion.

The method of coming to rest is somewhat peculiar. Pearl ('03) demonstrates it clearly in the case of *Planaria*, and as it is comparatively the same in the Phagocata I will quote: "The coming to rest is practically always preceded by a period of slower gliding, but all slow gliding is not immediately followed by rest. After a brief period of this slower gliding the worm suddenly stops, and the posterior half of the body remains fixed in precisely the same position. The anterior half of the body is slowly moved about over the bottom from side to side, the head being touched frequently to the bottom or any other solid objects in the neighborhood. The anterior part in this 'feeling' movement moves about the posterior part as a fixed point, the latter very rarely changing its position after it has once stopped. The apparent significance of the 'testing' movements at the time of stopping is that it is a piece of protective behavior."

In making experiments on regeneration, I have noticed several peculiar modifications in the movement brought about by the effect of the operations. Cross-sections at almost any part of the body seem to have but little effect upon the powers of locomotion of the head end. It swims about just as lively as ever, and responds to all the stimuli by which the normal animal is effected. The posterior part seems, on the other hand, to move much slower, and the nearer the cut approaches the posterior end of the body, the slower the movement. This piece is dormant at first, but later it moves at long intervals (providing the cut was not near enough to the tail end to kill it), remaining, however, for the majority of the time curled up in the dark corners of the aquaria and perfectly quiet. One specimen, which generated a second head as the result of an operation, seemed to be impelled to follow each head, and inasmuch as each head had a direction of its own, very little progressive movement was accomplished.

The *digestive system* of *Phagocata gracilis* as well as that of all other Triclad is a simple sac, opening to the outside in but one place. This opening—the *mouth*— is situated on the ventral surface of the body, usually a little back of the center and upon the median line. It can be seen in living specimens with the naked eye and appears as a very small opening surrounded by a dark ring of pigment (Plate I, Fig. 1, mo.). The opening in itself often does not appear to be as large in diameter as a single pharynx, and yet it can be expanded to a considerable size, even enough to permit more than twenty pharynges to be protruded through it at one time (Plate II, Fig. 17 C).

The mouth, exhibiting a gradual transition of epithelial cells, opens directly into a large chamber, the *atrium*, which contains the pharynges (Plate I, Fig. 11, p.at.). This cavity occupies about the middle third of the entire length of the body and also about one third of the width. At intervals *partitions* appear in it which seem to a certain extent to separate some of the pharynges from one another. These partitions arise as outgrowths of the lateral walls of the atrium, and extend for varying distances out into the cavity, usually inclining toward the mouth opening and joining to both dorsal and ventral walls throughout their entire length. Some gradually swing backward so as to run nearly parallel to the long axis of the body. These partitions serve as a support for the body-walls, and although they separate pharynges from one another, they converge or end in such a way as not to hinder them from reaching the mouth. In many places these partitions have just begun development, and appear as small projections extending out for short distances into the atrium from between the pharynges (Plate I, Figs. 1 and 9, pt.).

Scattered here and there between the pharynges and the partitions may also be found small outpocketings of the walls of the alimentary canal, which extend into the atrial cavity. They often appear in section to be similar to the partitions, but on following out their structure through successive sections they are found to be long conical outgrowths, each forming a blind sac. It has been shown by several writers that in cases of regeneration pharynges develop as outgrowths of the digestive tract, and there appears to be but little doubt that the outgrowths in question will ultimately break through at their outer ends and become functional pharynges (Plate I,

Fig. 1, r. ph.). The fact that the pharynges are constantly increasing in number as the animal grows older would corroborate this conclusion.

The *pharynges* are elongated, very muscular tubes which serve to secure food for the animal. They can, as mentioned above, be protruded to a considerable length from the mouth. The number varies in different individuals, ranging from fourteen to twenty-eight. I have tried to decide, by comparing many specimens, whether or not there is any definite number which can be considered as characteristic of the species, but the range is so varied that it seems almost impossible to come to any conclusion. It is quite certain, however, that the number varies according to the age of the animals, the youngest always having the least and the oldest the most. In regenerating *Phagocatae*, of course, any number up to the maximum may be found. One pharynx (Plate I, Fig. 1, a.ph.) is almost always larger than the rest, and connects with the alimentary tract at the juncture of the anterior and posterior trunks. The remaining ones enter the posterior tracts along their inner sides (Plate I, Fig. 1, l.ph.), growing smaller as they approach the posterior end of the body.

Each individual pharynx (Plate II, Fig. 31) in itself is highly specialized for its function. Both the muscular system and the cilia serve to draw in food from the outside, and so specialized is the pharynx in this duty that even when removed from the body it keeps up a vigorous swallowing. The end previously serving as the open or mouth end expands to a considerable size, envelops any particles with which it may come in contact, and then by muscular contraction (a sort of peristaltic movement) carries the food through the pharynx, only to be passed out of the other end. Dr. Woodworth has observed the movements of the pharynx when separated from the body and concludes that cilia bring them about, but, in so far as I can determine, nearly all movement under the circumstances is due to muscular contraction. Cilia, however, are present over much of the surface of the pharynx, and no doubt could be the cause of movement to some extent. About the mouth the cilia are much larger and serve to aid in getting food into the opening.

Structurally considered, the pharynx consists of seven layers which are, beginning with the outermost:

1. *External Epithelium* (Plate II, Figs. 22-24, e.ep.);



composed of columnar epithelial cells. Nuclei are usually invisible in the cells of fully grown pharynges except at the proximal end, but they may be observed on other parts of the pharynx. The external surface is almost entirely covered with cilia in the young pharynx except at the extreme proximal end. The cilia are often lost to a considerable extent in older pharynges, where the cells of the epithelium usually become distorted (Plate II, Fig. 23).

2. *Outer Longitudinal Muscle Band* (Plate II, Figs. 22-24, o.l.m.); usually narrow, but near the basal end of the pharynx it becomes much wider.

3. *Outer Circular Muscle Band* (Plate II, Figs. 22-24, o.c.m.); a wide band which has its fibers grouped into bundles arranged in feather-like clusters similar to those found in the musculature of the earthworm.

4. *Connective Tissue Layer* (Plate II, Figs. 22-24, c.t.); a wide zone of connective tissue containing various kinds of cells and muscle fibers. Many nuclei are found scattered throughout, and often numerous large ones adhere closely to the base of the circular muscle layer. A thick layer of nuclei is also found on the inner surface of the connective tissue which rests upon (5) the inner longitudinal muscle band. The transverse muscle fibers are commonly scattered, but they often run in regular bundles which seem, like so many septa, to divide the connective tissue area into several distinct parts.

5. *Inner Longitudinal Muscle Band* (Plate II, Figs. 22-24, i.l.m.); generally narrow but widening near the proximal end of the pharynx.

6. *Inner Circular Muscle Band* (Plate II, Figs. 22-24, i.c.m.); also of the feathery type similar to the external circular band, but so much more closely interwoven that the structure is often lost.

7. *Internal Epithelium* (Plate II, Figs. 22-24, i. ep.); formed of large columnar cells, which near the mouth of the pharynx are usually regular or often conical. Cilia are found lining the lumen for nearly half its distance back from the mouth. They are quite long in the neighborhood of the external opening. Where the cilia are missing the cells become irregular and the nuclei very noticeable.

The *digestive cavity*, as in other flatworms, has but a single opening to the exterior—the mouth. As in all Triclad the

cavity has three main branches, one running forward toward the head, and two passing backward to the tail region, giving the general appearance of a tuning-fork. The juncture of the three branches is about midway between the mouth opening and the head, and at this point enters the largest of the pharynges as mentioned above (Plate I, Fig. 1, a.t.r., l.t.r.). These main trunks give off smaller branches which extend throughout the body, and in this manner the food is distributed. The anterior canal runs forward through the central part of the body, somewhat toward the dorsal surface, and after passing over the brain turns directly downward and ends as a small canal close to the ventral surface. The branches here are much longer than those of the lateral tracts. The lateral tracts pass backward close along the atrial cavity and converge behind the genital pore so as to come close together in the tail region. The branches here are usually more simple than those of the anterior tract, and are found chiefly on the outer side of the two main trunks. In the extreme tail region a few very small tubes may be found outpocketing from the inner side, but these are mostly insignificant.

The prevailing idea according to statements and drawings on Planariidae is that the two posterior branches of the alimentary tract do not connect. In the case of Phagocata, however, I have found several toto mounts, as well as many sections, which show without the least bit of uncertainty a connecting tube from one of the posterior canals to the other in the tail region (Plate I, Figs. 1, 15, c.br.). Whether this transverse branch indicates the existence of a different variety of Phagocata, or whether it is simply a case in which two neighboring branches have by chance been fused end to end, I am at present unable to say.

The structure of the walls of the digestive tract is quite simple. It is composed of a single layer of rather large columnar cells which protrude into the cavity with somewhat irregular amoeboid-appearing surfaces (Plate I, Fig. 2, al.). If killed and sectioned directly after feeding, these cells are profusely filled with the food taken in, which is often in the shape of minute black granules. The nuclei are large, but not so large as many of those found in the mesenchyme, and rest near the bases of the cells. Occasionally there appear, scattered between the intestinal cells, large clear cells or cell spaces which contain

irregular black rods (Plate I, Fig. 2, i.c.s.). The function of the latter is not clear.

The *food* of the Planariidae is mostly animal matter, and the variety is very great. They will vigorously attack almost any kind of worm or insect which can be found in the water, and even while it is still alive will set about to devour it. In the absence of animal foods, small plants such as Diatoms and Bacteria are consumed. If a fly be dropped into an aquarium where there are Phagocatae, only a few minutes will elapse before it will be covered with the little animals. Whether it is by chance they come near the fly, or whether some sense is employed to discover it from a distance, is not evident, but they are certainly aware of its presence before they come in actual contact with it. I have seen them, with ventral side uppermost, gliding along the under surface of the water directly toward a fly, and, although half an inch from it, with numerous pharynges already protruded from the mouth, squirming about, ready to begin work (Plate II, Fig. 17, C). Several instances have been observed in which Phagocatae have devoured one another, but in each case great scarcity of food was the cause, and not any promiscuous cannibalistic habit such as has been found in some worms. The blood which the Phagocata sucks from its prey is often colored, and as a result it may take on a peculiar appearance. The whole alimentary tract may be colored a bright red, which shows up very plainly if the animal happens to be crawling on the sides of the aquarium. Sometimes only certain of the pharynges will obtain the colored food and, in passing it on, that part of the intestine only which is in close contact with these pharynges will be colored, and thus a very striking appearance is given.

In the absence of food Phagocatae can live for varying lengths of time, depending on the condition of the water in which they are confined. Out of eighteen specimens kept in filtered water, only two lived for fifty days. The number began to decrease rapidly after the thirtieth day, and upon careful observation I at last found several of the animals busily devouring one of their companions. On the forty-fifth day but three were left, and during the same night one of these disappeared. Upon the fiftieth day the remaining two, although apparently well supplied with food for some time, secreted about themselves a mucus cyst, and after several weeks seemed to disintegrate

and disappear entirely. In hydrant water the conditions are greatly changed, due to the fact that the animals can obtain a considerable amount of food from the bacterial scums. They seem to be able to live indefinitely in this condition, and the only apparent effect is that they gradually grow smaller, due to the scarcity of food.

As there are no special *respiratory organs* present, all the oxygen absorbed by the Phagocata must be taken in through the body wall. The ectoderm here, as in the case of so many of the lower animals, is said to perform this function. The cilia, so numerous over much of the body, are constantly moving, and will thus keep the water in motion and have fresh oxygen always in contact with the ectodermal cells.

The *nervous system* is composed of a brain, located in the head; two main nerve trunks running parallel to the long axis of the body; and a lateral network of fibers, often considered a second series of trunks.

The *brain* (Plate II, Figs, 25, 26, 27), located toward the posterior part of the head region, is formed by the union of the main nerve trunks. It consists of two lobes, one on either side of the median line, and a dense mass of connecting fibers, which appears, from frontal and transverse sections, to be divided into four bundles. Woodworth ('91, p. 29) mentions only the antero-posterior division into two commissures (Plate II, Fig. 25) and fails to consider the distinct division into dorsal and ventral parts which is clearly shown in cross-sections (Plate II, Fig. 27). Fig. 26 also shows the beginning of a division into dorsal and ventral parts within the lobe. Each lobe is deeply indented from above and from below by conical projections of what is presumably connective tissue which extend nearly to the center of the mass.

There are two distinct nerve trunks (Plate II, Fig. 26) arising from the anterior half of each brain lobe and extending forward. The upper or dorsal bundle is much the larger and is the only one commonly recorded. It is composed of several collections of fibers, which soon split up and extend to all parts of the head. One comparatively large mass of fibers from this trunk innervates the eye. The lower or ventral bundle arises by two roots from the anterior half of the brain lobe, and runs along the lower surface of the head to which it gives off many small branches.

The two main *nerve trunks* of the body pass out of the posterior part of the brain lobes midway or somewhat toward the dorsal side, but soon curve downward and come to lie close to the ventral surface. They run practically parallel to the lateral walls of the body, passing outside of the atrial cavity and converging again in the tail region. Each trunk in itself is made up of two series of fibers, slightly separated and having many intercrossing branches. The texture of the fibers is not visible under comparatively high magnification. Numerous branches are given off from the main cords, some of which pass inward and interlace with each other or occasionally join near the median line, while others pass outward toward the periphery and are united to a certain extent near the edges of the animal into two series of fibers which are called the marginal or peripheral cords. A considerable amount of the ventral part of the body just within the musculature is filled with a fine network of fibers which branch and unite so as to form a complex system having the peripheral cords as their outer terminals. In the region of the tail this network becomes very noticeable, and especially so about the genital pore (Plate II, Fig. 29, g.p.). This last mentioned system of fibers is the so-called ventral plexus which Woodworth ('91) observed in *Planaria abscissa*.

Of the *special senses* Phagocatae appear to have at least three, with the possibility of a fourth. Sight, which we will consider first, is but partially developed, in that the animal can only distinguish between light and dark and apparently does not observe solid objects until it comes into actual contact with them. The *eyes* are situated in front of the brain, one being on each side of the median line. Under the microscope they appear to be composed of two parts, an inner black knot of fibers, surrounded by an outer clear space (Plate II, Fig. 28). The inner part is composed of a very dense opaque tissue which in places appears slightly fibrous. It is either oval or slightly crescentic, and is often cup-shaped. It is always located toward the inner part of the clear space, and when in form of a crescent the convex side is toward the median line of the body. The outer or clear part of the eye is marked by the absence of pigment either in its own tissue or that of the body covering about it. Under very high magnification this clear space shows the presence of many fine colorless nerve fibers. A certain part of it is hidden by the dark portion of the eye which gives

it the appearance of a large clear crescent with its horns pointing inward.

The *sense of touch* is probably the most highly developed of all the special senses, the complex ramifications of the nervous system reaching to all parts of the body. Even the slightest mechanical stimulus at almost any point will call forth a direct reaction. The head end is by far the most sensitive, however, and it is by means of this organ that the animal "feels" its way about. Great numbers of fine fibers run from the brain to the surface of the head, forming a large fan-like structure, thus indicating a high development of the tactile sense in this region.

Besides the above-mentioned senses, Phagocatae exhibit the presence of still another special sense. We know that the animals have a very keen selective capacity in that they much prefer some foods to others. Moreover, the recognition of the presence of food while at a distance (which has already been discussed under digestion) shows the presence of a special perceptive mechanism for this function. There is still some doubt as to whether we are to consider these two responses as one and the same or not. It seems probable, however, that the powers of *tasting* and *smelling* are both present in a primitive condition.

Like almost all other low forms, Phagocatae show no apparent recognition of any kind of sound.

Inasmuch as my results on the *reproductive system* of Phagocata gracilis vary so extensively from those of Woodworth ('91) on the same species, and likewise from the general ideas concerning this system in many of the flatworms, I have striven to work it out in great detail.

Phagocatae, like all other Turbellaria except Stenostomum, Microstomum, and Plagiostomum diocum, are hermaphroditic. Although both male and female cells are present in the same individual, self-fertilization must be very rare, if present at all, as the ova and spermatozoa do not mature at the same time in the same individual.

The female reproductive organs (Plate II, Figs. 19, 32, 33) consist of (1) two ovaries, in the anterior part of the body; (2) two oviducts, leading backward and uniting to empty into the muscular tube close to its entrance into the genital atrium; (3) a large, irregularly formed organ called the uterus, resting anterior to and somewhat above the large pear-shaped sperm receptacle; (4) a uterine duct, connecting the uterus with the

genital atrium, which, in turn, opens to the exterior by means of the genital pore; (5) parovaria and yolk glands.

The *ovaries* are two in number and are located in the anterior third of the body, a short distance in front of the first pharynx and immediately central to the longitudinal nerve cords (Plate I, Fig. 6, ov.). They rest close to the ventral surface of the body below the large branches of the alimentary canal. The individual ovary (Plate II, Fig. 19) is a somewhat rounded structure, four or five times the size of the ordinary spermary. It is bounded by a very narrow layer of fibrous tissue which usually adheres so closely to the surrounding connective tissue that it is often overlooked. Various stages of developing ova may be seen within one ovary. Around the outer edges are gathered the earliest stages, and the more mature ova are often scattered loosely within the center of the mass. Oogenesis appears on superficial examination to be similar to that found by Child ('07) in *Moniezia*, except that as yet no cases of mitosis have been observed. Amitotic divisions are fairly common.

The *Oviducts* are two in number, one opening from the posterior or slightly to one side of each ovary (Plate II, Fig. 19, od.), and passing backward close to the two main nerve trunks. Directly above the region of the genital atrium they unite to form a single duct, which immediately turns downward and empties into the muscular tube of the male genital system a short distance from where this organ enters the genital atrium (Plate II, Figs. 32, 33; Plate III, Figs. 45, 64, od.). The condition here agrees in most respects with that recorded for *Planaria alpina* and *Planaria torva*. In these forms the common oviduct is shown as entering the genital atrium at a considerable distance from the opening of the uterine duct, and quite close to the penis (Gamble, '01). In *Phagocatae* the muscular tube is to be considered as an extension of the genital atrium, and so the similarity is apparent. Woodworth ('91) describes this duct as opening into the vagina (uterine duct) close to its entrance into the genital atrium<sup>1</sup>, but in my specimens, at least, this is not the case.

Structurally considered each oviduct is made up of a single

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1. This condition is also given for *Planaria polychroa* where the oviducts enter the uterine duct separately, and in *Gunda ulvae* where they enter after uniting (Gamble, '01).

layer of closely set cells surrounded by a delicate basement membrane which seems to rest directly upon the cells of the surrounding mesenchyme (Plate II, Fig. 36).

The so-called *uterus* (Plate II, Fig. 32, 33 ut.), which is the same as that designated by other writers under the same name, is an irregular, often somewhat club-shaped sac lying directly anterior and somewhat dorsal to the sperm receptacle, and occupying the space between that organ and the pharyngeal atrium. It often projects forward into the posterior part of the pharyngeal cavity, as is shown in transverse sections through this region (Plate I, Fig. 11, ut.). Histologically considered the uterus is quite simple, consisting of two layers only. The inner or epithelial lining is composed of rather large, irregular, pyriform cells which are more or less granular, strictly suggesting glandular tissue. The outer layer is a thin structureless band which is continuous with the muscular coat of the uterine duct. As Woodworth ('91) has said, a greater variety of ideas exists concerning the uterus of flatworms than any other structure of the body of these forms. In *P. gracilis* he finds it to be glandular in structure and also a receptacle for both spermatozoa and ova, and believes that fecundation takes place there. Up to the present time, however, I have been unable to determine the presence of any spermatozoa in the uterus, and in but one preparation have I chanced upon anything which might be taken for developing eggs. In this case two large bodies were present, but because of excess of stain nothing of their structure could be observed.

The fact that no definite eggs have been found within the uterus and also the well proven conclusion that the oviducts in Phagocatae, as well as in several other similar forms, do not empty into the uterine duct at all but instead lead to the genital atrium, have brought up again the old question, does the uterus of the Planariidae function as a receptacle for ova and developing eggs? This question will be discussed more thoroughly in a later paper, but at present it will be well to say that it is difficult to see how the so-called uterus, in Phagocata at least, can serve as such, when one considers the general anatomy of the reproductive system. The eggs in this form, as well as those mentioned above as showing a similar condition, would be obliged to pass from the oviducts into the muscular tube of the male genital system and thence into the genital atrium before entering the uterine duct. The genital atrium is a chamber



connecting directly with the exterior, and therefore the ova must pass almost to the outside of the body and then be withdrawn again by some unexplained power of the uterine duct (that this condition would of necessity follow can be readily seen by a reference to Plate III, Fig. 64). It may be argued that the cilia within the lumen of the uterine duct could bring this about, but when one considers that these cilia are only present in the proximity of the uterus proper and at a considerable distance from the mouth of the duct, it seems improbable that they can be responsible for the withdrawal of the ova from the genital atrium. So it would seem from the above facts that either the function of the so-called uterus in these forms has been radically mistaken or that there still remain other factors, not yet discovered, which will explain how the uterus or its accompanying duct is able to remove the ova from the genital atrium. As a suggestion it might be well to mention here the possibility that this so-called uterus may serve as a receptacle for spermatozoa, as Kennel ('88, p. 458) has found in certain Turbellaria; or, as is suggested by its glandular structure, it may serve as an organ for the secretion of the cocoon, as is recorded by Iijima ('84) in fresh-water Triclad.

The uterus, as already indicated, connects with the genital atrium by means of the *uterine duct*.<sup>1</sup> This passes backward from the uterus close to the dorsal surface, above and to the left of the sperm receptacle, and finally turns directly downward and empties into the genital atrium just to the left of the muscular tube (Plate II, Fig. 32). There is no definite muscular sac here as is shown in *Dendrocoelium lactea* and *Planaria torva*. The structure of the uterine duct has been well worked out by Woodworth ('91, p. 36), who says, "Where the vagina arises from the uterus it is lined with a ciliated epithelium of low cubical cells, and possesses a musculature of circular and longitudinal fibers. As it passes backward, the cells of the lining epithelium become taller and cylindrical, and the nuclei are elongated (Plate II, Fig. 34). The outer ends of the cells show distinct granulations, and the contour of the lumen becomes uneven; the granular nature of the cells now becomes apparent. Along with the change in appearance of the cells of the lining epithelium there is an increase in the thickness of the muscula-

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1. Woodworth has termed this duct the "vagina."

ture, which now consists of alternating layers of circular and longitudinal fibers. The musculature of the vagina reaches its greatest development at the point where it bends toward the ventral side of the body; from this point onward the cells lose their granular character, and the musculature diminishes in thickness, till, at the point where the vagina receives the oviducts, it again consists of only a single layer each of circular and longitudinal fibers."

The *genital atrium* (Plate II, Fig. 32; Plate III, Figs. 48, 64, g. at.) is a rather small cavity formed by the union of the muscular tube and the uterine duct. It lies close to the ventral surface, to which it opens by means of the *genital pore* (Plate III, Fig. 64, g.p.). The lining is of epithelial cells which show a marked transition between the cubical cells of the ventral epithelium and the long pyriform cells of the muscular tube and uterine duct.

The *yolk glands* (Plate II, Fig. 30) are periodical in their appearance, and it was not until after many attempts that I could find material which corroborated Woodworth in his conclusions concerning them. They first appear near the anterior part of the body as small groups or chains of cells which gradually increase in size and number so as to occupy a considerable space. The individual cells are large and irregular, and contain heavily granulated nuclei. As yet I have not been able to find anything which corresponds definitely to the parovaria mentioned by Woodworth. According to that author a large mass of cells (parovaria), the function of which is to supply material to the yolk glands, is to be found encircling three sides of each ovary. Holding in mind, however, the fact that it took me so long to come to a common conclusion with Woodworth concerning the yolk glands, I have refrained from drawing any conclusions upon the parovaria, which he maintains are closely related to these glands.

The male sexual organs consist of (1) numerous small testes scattered throughout nearly the whole extent of the body; (2) minute, practically unrecognizable spermatid ducts leading from the testes to the vasa deferentia; (3) the two vasa deferentia for collecting the spermatozoa and conducting them to (4) the large muscular sperm receptacle in which are stored the fully developed spermatozoa; (5) the penis, contained in the lower chamber of the sperm receptacle and opening directly into

(6) a large muscular tube which connects with (7) the genital atrium; and (8) the genital pore.

The *testes* (Plate I, Figs. 1-16, sp.) are very numerous and are widely scattered, ranging from directly behind the brain to the tip of the tail. They are found in the mesenchymatous tissue filling in the spaces between the branches of the digestive system, and, though some may be located toward the dorsal side, the great majority are found nearer the ventral surface. This somewhat ventral location of the testes seems to be directly opposed to the general conditions recorded for other flatworms. Woodworth ('91, p. 31) finds that after the mature spermatozoa have found their way to the vasa deferentia all traces of the testes disappear. I have not found this to be the case in my material. Every section that I have made, no matter at what time of the year the material was collected, shows the presence of many testes.

In early stages the testes may be found appearing as small clumps of cells, often not more than two or three in number, which are scattered throughout the mesenchyme. By means of division, which, as in the case of the ova, is apparently amitotic, these few cells multiply and form clumps of comparatively large, highly chromatic cells, which I have concluded are of the spermatogonial type (Plate II, Fig. 18, sp'ga.). Shortly after this stage is reached many cells may be found in which the chromatin has collected into masses which may represent symapsis. Following this, in some cases the granules seem to collect more markedly about the walls, and the cells as a whole become somewhat elongated and barrel-shaped (Plate II, Fig. 18, S-1). This condition seems to be a preparation for an amitotic division which follows. In other cases definite chromosomes (Plate II, Fig. 18) may be seen which divide mitotically. These divisions give rise to large masses of cells which are highly chromatic and evenly granulated (Plate II, Fig. 18, S-2). Following this stage enters a series of divisions which in many cases are apparently amitotic in character and which result in still smaller cells having a clear cytoplasm and large deeply staining nuclei. These are apparently the spermatids (Plate II, Fig. 18, sp'td.), and every stage of intergradation can be found between them and the mature spermatozoon (Plate II, Fig. 18, sp'za.). The nucleus of the spermatid appears to become elongated and pointed at one end, and at this end the tail of

the spermatozoon is formed. The cytoplasm remains surrounding the bulk of the nucleus, but on account of the increase in size of the latter, the cell wall comes to lie so close to it that often all traces of the achromatic tissue are lost. The head of the spermatozoon then elongates markedly, and the cells come to lie in massive clumps about characteristic nurse cells which are located near the center of the spermary. All of the foregoing stages may be found within a single spermary, as is shown in Fig. 18 of Plate II, but on account of the minuteness of the cells I have found it quite difficult to determine the characteristic stages of spermatogenesis.

It has proven practically impossible to trace the course of the spermatozoon from the testes to the vasa deferentia. Many of the spermaries, however, have been found to show elongations of their surrounding walls which become smaller and smaller as they recede from the body of the testes and finally disappear. These in all probability are to be considered the *sperm ducts*.

Lying along the outside of the pharyngeal cavity, on either side, and close to the ventral wall, may be found the two *vasa deferentia* (Plate II, Figs. 32-33, vd.). Each duct originates as a comparatively large tube somewhat near or a little anterior to the mouth, and in passing backward gradually decreases in size until it reaches the region of the uterus. From here it passes still farther on toward the tail end, parallel with the corresponding duct of the opposite side, and finally when close to the apex of the sperm receptacle, turns inward and upward to enter the base of the latter on its lateral surface. This account of the course of the vasa deferentia is directly opposed to that of Woodworth ('91, p. 31), who says, "They (vasa deferentia) run backward parallel to each other until near the base of the penis; they then turn at right angles toward the middle plane, where they unite to form a single tube which terminates at the apex of the penis (sperm receptacle)." Not one of the several hundred specimens which I have prepared shows any exception to the course which I have described for the vasa deferentia, and in no case can I find any trace of these ducts turning at right angles in the vicinity of the "penis" and joining into a single duct to enter the apex of that organ.

It is with regard to the so-called "penis," however, that my observations differ most extensively from those of most other investigators upon the same or allied species. The large

pear-shaped structure which is termed the penis in so many flatworms is present in *P. gracilis* and is described by Woodworth ('91, p. 32) as being very similar to that of *Planaria polychroa*: "The penis or intromittent organ is a highly muscular plug-like structure that lies in the genital atrium or penis sheath. It is covered with flattened epithelium, under which there are alternating layers of circular and longitudinal muscles, five of each, forming a thick zone. Immediately outside of the epithelial lining of the tube there is a band of circular muscles, and between these and the outer muscles there is a broad zone occupied by a meshwork of muscular fibers, prominent among which are those having a radial direction. The lumen of the penis is not of an even calibre, but consists of a succession of chambers, or dilations, lined with a granular epithelium, which is probably glandular. . . . The sheath of the penis is lined with an epithelium of cylindrical cells, the nuclei of which lie close to the bases of the cells, and are stained deeply, while the glandular cell substance is stained only slightly."

The above description agrees, as far as it goes, with my results, except that in the place of the five alternating layers of circular and longitudinal muscles, I find simply a broad band of muscular tissue which shows but little differentiation. Woodworth has, however, omitted several important details concerning the structure of this organ.

It is evident in *Phagocata gracilis*, and I am inclined to believe this will be found to be true in many other flatworms, that what is usually called the penis is in reality a large muscular organ which contains within itself both the true penis and certain enlargements for the purpose of storing up mature spermatozoa.

The vasa deferentia do not enter, as described by Woodworth, by a common duct at the base of the "penis," or *sperm receptacle* as I shall term it from now on, but through separate openings on opposite sides of that organ (Plate II, Fig. 33; Plate III, Fig. 50, v.d.). Their points of entrance are quite close to the most anterior extremity, where the muscular tissue of the organ projects forward and attaches to the ventral wall of the body. They pass down through the anterior half of the sperm receptacle, which is composed of irregularly arranged muscular and connective tissue, and, converging so as to lie close to one another, enlarge suddenly to a considerable size,

to finally unite and empty directly into the anterior seminal chamber by a single duct (Plate II, Fig. 33; Plate III, Figs. 53-56, v.d.i.).

The *anterior seminal chamber* (Plate II, Fig. 32,33; Plate III, Figs. 38-43, 53-57, a.c.) is the largest of three chambers which occupy the greater part of the distal half of the muscular sperm receptacle. It begins as a narrow opening close to the dorsal wall of the receptacle about three fifths of the distance from its proximal end. As it passes backward, occasionally a little to one side of the median line, it enlarges until it occupies the greater part of the diameter of the receptacle, and then pinches off into two slender tubes which empty into the posterior seminal chamber (Plate III, Fig. 58, c.).

The *posterior seminal chamber* (Plate II, Figs. 32-33; Plate III, Figs. 43-59, p. c.) is much like the first, except that it is smaller, and more centrally located. Both of these chambers are surrounded by a clear strip of muscular tissue, and their lumens are lined with an irregularly scattered, granular epithelium. A single duct leads backward from the posterior seminal chamber and is continuous with the lumen of the penis. This duct is quite convoluted, and in sections often appears like several enlargements instead of a continuous tube (Plate III, Fig. 43, d.).

A third chamber (Plate II, Fig. 33; Plate III, Fig. 44, p.s.) is present which at first glance might be mistaken for an additional seminal chamber. It is, however, an extraneous chamber which in reality surrounds the penis, being an invagination of the distal end of the sperm receptacle to form a *penal sheath*. The muscular walls of this chamber are continuous with the external musculature of the receptacle proper and connect by a ligament-like structure (Plate III, Fig. 45, a.) to the walls of the main sheath surrounding the sperm receptacle. This attachment serves as a hold fast which anchors the penal sheath when the penis is protruded.

The *penis* (Plate II, Figs. 32, 33; Plate III, Figs. 44, 60, pe.) is attached anteriorly to the base of the penal sheath by a strong muscular band and is traversed by a single duct which is continuous with the lumen of the posterior seminal chamber. Structurally the penis is composed of a dense muscular tissue and is covered externally by a fine, irregular epithelial layer whose cells give the organ an uneven knotty-appearing surface.

The penis of *Phagocata* does not at any time turn inside out, as it were, but is an organ of fairly constant form. Protrusion is accomplished by contraction of the walls of the sperm receptacle, which in turn forces the distal end of that organ farther from its point of attachment. Through this contraction the receptacle itself is lengthened, and inasmuch as ligament-like structures bind the walls of the penal sheath tightly to the sides of the main sheath of the receptacle, an evagination of the end of the receptacle results, and thus a protrusion of the penis is accomplished.

Benedict ('00, p. 363) in a fish tapeworm of the Genus *Proteocephalus* describes the manner in which the cirrus is protruded, and it is quite similar to my observations. "The mechanism for protrusion seems to be as follows: The longitudinal muscles of the cirrus sac, which are reflected at the distal end of the pouch into the walls of the inner tube, by contraction, would evaginate that distal portion of the tube which is free from the cirrus, and pull the rest of the inner tube outward through the sac, stretching the 'roots'. The evaginated distal portion of the tube forms the muscular protuberance, the former rough cuticular lining of which is now on the outside. Retraction would be accomplished principally by the roots, which, as has been seen, are attached to the proximal end of the inner tube."

Benedict also shows a structure in the case of the penis and its associated organs which is much like that I have described for *Phagocata gracilis*. He says: "The cirrus sac is an elongated oval in shape, slightly constricted in the middle. It extends from the edge of the genital pore to the median dorsal line of the parenchymal space, where a number of heavy muscle strands attach the proximal end of the inner tube of the pouch firmly to the dermo-muscular sac. . . . At the anterior end the wall of the pouch bends back, forming a tube through the middle of the sac. This tube is lined in the distal half, by cuticula, which is continuous with that covering the surface of the body. . . . At the proximal end the free cirrus enters a muscular protuberance of the shape of a truncated cone . . . . The cirrus passes through the center of this and back through the pouch in very intimate connection with the walls of the inner tube of the sac." As may be readily seen from the quotation, the cirrus pouch differs

considerably from the organ I have termed the sperm receptacle, but the penis and its attachment as well as its manner of protrusion is strikingly similar to that found in Phagocata.

Lastly among the male genital organs is the *muscular tube*<sup>1</sup> (Plate II, Figs. 32, 33; Plate III, Figs. 40-47; 53-64, m.s.), which connects the sheath-cavity of the sperm receptacle with the genital atrium. It may spring either directly from the posterior end of the sheath (Plate III, Fig. 45, m.s.) or, more frequently, a considerable distance forward on the ventral side (Plate III, Fig. 54, m.s.). It passes backward to the right of the uterine duct, turns downward, and empties into the dorsal surface of the genital atrium. The structure of the muscular tube is quite similar to that of the uterine duct, except that it is somewhat oval instead of circular in shape and is in nearly all parts considerably larger in diameter.

Regeneration in *Phagocata gracilis* is not greatly different from that found in practically all the other members of the Planariidae, and as this subject is to be treated in a later paper it will be omitted here.

BIOLOGICAL LABORATORY,

*University of Cincinnati, March 11, 1910.*

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1. The organ which is here termed the muscular tube appears to be an anterior extension of the genital atrium as described by other writers, but because it has been extended into such an elongated tube it has seemed permissible to apply the above-mentioned name.



## METHODS

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It may be well to mention here some of the methods which have been employed in preparing specimens for investigation.

First of all it is necessary to say that much better results have been obtained in all cases where the animals have been kept confined in clear water, without food, for a few days previous to killing.

Many killing and fixing fluids have been used, the most important of which are: Hermann's, Merkel's, acetic alcohol, Zenker's, Fleming's, formalin, alcohol, Gilson's mercurio-nitric, etc. Of these Merkel's fluid—

Chrom-platinic mixture:

Chromic acid (1% aq. sol.)	25 c.c.
Platinic chloride (Pt Cl <sub>4</sub> ) 1%	25 c.c.
Distilled water	150 c.c.

and Gilson's

Mercurio-nitric fixing fluid:

Bichloride of mercury	5 g.
Nitric acid (80%)	4 c.c.
Glacial acetic acid	1 c.c.
Alcohol (70%)	25 c.c.
Distilled water	220 c.c.

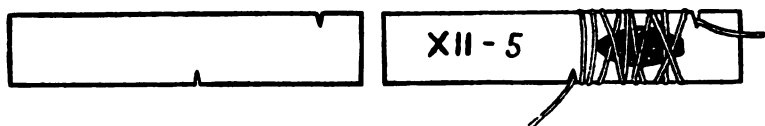
are by far the most satisfactory in working with Phagocata.

The Gilson's mixture is probably the most reliable. It kills and fixes the tissue readily and is followed well by almost any stain. To kill with this fluid it is generally recommended that the mixture be heated, but in the case of Phagocata I find that heat seems to cause a curling, and also the secretion of a dense mucus. Both of these objections are eliminated by simply flooding the slide, upon which an animal is swimming in a few drops of water, with cold Gilson. The animal curls up for a second or two and then gradually straightens out to a perfectly flat condition. At this point a cover-glass is dropped upon the body and the slide cover, worm, and all are immersed in the killing fluid for about ten minutes or longer; thence transferred to 50 per cent alcohol, to which a few drops of iodine have been added in order to remove the excess of mercuric chloride.

For toto mounts Guyer ('06) has offered the following method which has given some good results:

Kill with hot Gilson's,<sup>1</sup> 10-15 min.; wash in 50% alcohol to which a few drops of iodine have been added, 30 min.; stain in weak Borax Carmine or Delafield's Hematoxylin (one of stain to fifteen of water) 24 hrs.; wash in water; decolorize in acid alcohol; dehydrate; flatten by compression between two slides (fasten with rubber bands) and harden for 24 hrs., in 95% alcohol; absolute alcohol 1 hr.; xylol 1 hr. or until clear; mount in Canada balsam.

For sectioning, especially where frontal sections are desired, great difficulty is experienced in keeping the specimens from wrinkling and curling while in the xylol and paraffin. I was practically unable to obtain a complete frontal section of any kind until I hit upon the following simple method. The worm is taken from 95 per cent. alcohol and placed, dorsal surface up, upon a small piece of cardboard about  $\frac{1}{4}$  inch wide by  $1\frac{1}{4}$  inches long, upon the sides of which two small slits have been cut some half an inch apart. A piece of fine thread or pre-



ferably an easily broken raveling from a piece of common cheese-cloth is caught in one of the slits and then wound over and over the entire body of the worm, to the other slit in which the loose end is caught. In this condition the preparation is carried through absolute alcohol, xylol, and the paraffin bath. To imbed, cut along the edge of the cardboard with a pair of sharp scissors (thus cutting all the threads at once) and remove the tissue to the embedding L's.

The paraffin used varies according to the thickness of the sections desired. Hard paraffin (62 degrees) is necessary to get very thin sections, whereas that melting at 45-50 degrees is best for thick topographical sections. Because of the brittleness of the tissue it has been found of great advantage to use Johnson's-Paraffin-Asphalt-Rubber method.<sup>2</sup> The imbedding

1. Cold Gilson has been substituted for the hot in this method.

2. Guyer: *Animal Micrology*, p. 44, or Johnson: *Journal of Applied Microscopy*, Vol. VI, p. 2662.

mass consists of one part of crude India rubber cut into very small pieces, mixed with ninety-nine parts of hard paraffin which has previously been melted and tinged to a light amber color with a small amount of asphalt ("mineral rubber"), and subjected to a temperature of not over 100 degrees for from 24 to 48 hours.

The stains used have been of various kinds, and space permits the mention of only a few of the best. The two most commonly used have been Delafield's Hematoxylin counterstained with eosin, for general structure, and Heidenhain's Iron Hematoxylin followed by Bordeaux red or Orange G. as a cytoplasmic stain, for more minute details. Van Gieson's Picro-fuchsin is very serviceable in bringing out the muscular system and connective tissue. Lyons blue, gentian violet safranin, carmalum, hemalum, borax carmine, picric acid, acid fuchsin, and many others have been found to be quite serviceable stains in control material.

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## EXPLANATION OF FIGURES

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<i>a.</i>	Attachment of sperm receptacle to sheath.	<i>m. s.</i>	Muscular tube.
<i>a. c.</i>	Anterior seminal chamber.	<i>mus.</i>	Muscular system.
<i>a. co.</i>	Anterior commissure.	<i>o.</i>	Ova.
<i>al.</i>	Alimentary canal.	<i>oc.</i>	Eye.
<i>am.</i>	Amitosis.	<i>oc. c.</i>	Clear parts of eye.
<i>a. ph.</i>	Anterior pharynx.	<i>o. c. m.</i>	Outer circular muscles.
<i>a. tr.</i>	Anterior intestinal tract.	<i>oc. p.</i>	Pigment of eye.
<i>b. m.</i>	Basement membrane.	<i>od.</i>	Oviduct.
<i>br.</i>	Brain.	<i>od. 2.</i>	Tube formed by union of the two oviducts.
<i>c.</i>	Connection between anterior and posterior seminal chambers.	<i>o. l. m.</i>	Outer longitudinal muscles.
<i>c. br.</i>	Connecting branch between intestinal tracts	<i>ov.</i>	Ovary.
<i>cil.</i>	Cilia.	<i>p. at.</i>	Pharyngeal atrium.
<i>c. t.</i>	Connective tissue.	<i>p. c.</i>	Posterior seminal chamber.
<i>d.</i>	Duct leading from posterior seminal chamber to penis.	<i>p. co.</i>	Posterior commissure.
<i>d. c. m.</i>	Dorsal circular muscles.	<i>pe.</i>	Penis.
<i>d. co.</i>	Dorsal commissure.	<i>ph.</i>	Pharynx.
<i>d. ep.</i>	Dorsal epithelium	<i>p. n. c.</i>	Peripharal nerve cord.
<i>d. l. m.</i>	Dorsal longitudinal muscles.	<i>p. s.</i>	Penal sheath.
<i>d. v. m.</i>	Dorso-ventral muscles.	<i>pt.</i>	Partitions.
<i>e. cil.</i>	External cilia.	<i>rh.</i>	Rhabditi.
<i>e. ep.</i>	External epithelium.	<i>rh. c.</i>	Rhabditi matrix cell.
<i>ep.</i>	Epithelium.	<i>r. ph.</i>	Rudimentary pharynx.
<i>g. at.</i>	Genital atrium.	<i>s.</i>	Sheath of sperm receptacle.
<i>g. p.</i>	Genital pore.	<i>s-1. }</i>	Two different stages in spermatogenesis.
<i>i. br.</i>	Intestinal branches.	<i>s-2. }</i>	
<i>i. cil.</i>	Internal cilia.	<i>s. m. s.</i>	Sub-muscular spaces.
<i>i. c. m.</i>	Internal circular muscles.	<i>sp.</i>	Spermmary.
<i>i. c. s.</i>	Intra-cellular spaces.	<i>sp'ga.</i>	Spermatogonia.
<i>i. ep.</i>	Internal epithelium.	<i>sp. r.</i>	Sperm receptacle.
<i>i. l. m.</i>	Internal longitudinal muscles.	<i>sp'id.</i>	Spermatids.
<i>in.</i>	Intestine.	<i>sp'za.</i>	Spermatozoa.
<i>l. br.</i>	Lateral nerve branches.	<i>ut.</i>	Uterus.
<i>l. n. c.</i>	Longitudinal nerve cord.	<i>ut. d.</i>	Uterine duct.
<i>l. ph.</i>	Lateral pharynges.	<i>v. b. w.</i>	Ventral body wall.
<i>l. tr.</i>	Lateral intestinal tract.	<i>v. c. m.</i>	Ventral circular muscles.
<i>mes.</i>	Mesenchyme.	<i>v. co.</i>	Ventral commissure.
<i>mo.</i>	Mouth.	<i>vd.</i>	Vas deferens.
		<i>vd. i.</i>	Vasa deferentia within the sperm receptacle.
		<i>v. l. m.</i>	Ventral longitudinal muscles.

## PLATE 1

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- Fig. 1. Camera lucida drawing of a toto mount of *Phagocata gracilis* showing the general arrangement of the body regions and parts of the nervous, digestive, and reproductive systems, X 12.
- Fig. 2. Portion of a cross section showing the general structure of the worm, X 200.
- Figs. 3-16. Series of cross sections taken at intervals throughout the entire body, X 18.
- Fig. 3. Cross section close to the anterior margin of the body showing a large amount of sub-muscular spaces.
- Fig. 4. Cross section through the eyes; part of the brain and anterior tip of the alimentary canal are also visible.
- Fig. 5. Cross section through the center of the brain showing its two lobes and their connection.
- Fig. 6. Cross section through the region of the ovaries.
- Fig. 7. Cross section somewhat back of the ovaries showing the large anterior tract of the intestine; also intestinal branches, lateral nerve cords, oviducts, and testes.
- Fig. 8. Cross section through region of the anterior or primary pharynx and beginning of the two lateral intestinal tracts.
- Fig. 9. Cross section showing the three anterior pharynges and some of the partitions which are found in the pharyngeal cavity.
- Fig. 10. Cross section through the region of the mouth showing sections of several pharynges, one of which is protruding from the mouth. Also shows how the intestine is pushed out toward the lateral walls of the body.
- Fig. 11. Cross section through the posterior part of the pharyngeal atrium showing the uterus pushed forward dorsally over a part of the cavity. The oviducts and vasa deferentia are also visible.
- Fig. 12. Cross section through the upper part of the sperm receptacle showing the cavity and sheath which surrounds this organ, the uterine duct, oviducts, vasa deferentia, spermaries, and part of the alimentary canal.
- Fig. 13. Cross section through the posterior part of the sperm receptacle showing the anterior seminal chamber and the opening of the muscular tube into the cavity surrounding the receptacle.
- Fig. 14. Cross section through the genital pore. The two lateral branches of the intestine are still visible.
- Fig. 15. Cross section in the tail region showing a connecting branch between the two lateral branches of the intestine.
- Fig. 16. Cross section in the extreme posterior region showing again the large sub-muscular spaces.

## PLATE 2

- Fig. 17A. Slightly enlarged drawing of a *Phagocata* as viewed against the light.
- Fig. 17B. Various forms assumed by the worms when at rest.
- Fig. 17C. Ventral view showing several pharynges protruded from the mouth at one time; X 3.

- Fig. 18. Portion of a transverse section of a spermary showing many of the details of spermatogenesis, X 1000.
- Fig. 19. Cross section of an ovary showing various stages in the development of the ova, X 350.
- Fig. 20. Shows a characteristic cyst containing several worms attached to the under surface of the water, X 1.
- Fig. 21. Individual cysts, X 1.
- Figs. 22-24. Three longitudinal sections through the wall of a pharynx taken at intervals between the distal and proximal ends respectively, X 450.
- Fig. 25. Frontal section of brain showing the two lobes, their anterior and posterior commissures, the branches to the head, and the beginning of the two main nerve trunks, X 225.
- Fig. 26. Sagittal section through one of the brain lobes showing the outgoing nerves to the head and body, the connective tissue indentations, etc., X 450.
- Fig. 27. Transverse section of brain showing general structure and division into dorsal and ventral commissures, X 225.
- Fig. 28. Transverse section through an eye showing the dark part cut near the outer edge of the cup, and the fibrous condition of the outer or clear tissue, X 50.
- Fig. 29. A frontal section near the ventral surface in the region of the genital pore showing the two peripheral cords and their interlacing branches, X 15.
- Fig. 30. A yolk gland, X 250.
- Fig. 31. Longitudinal section through one of the larger pharynges showing the general structure of the entire organ, X 87.
- Fig. 32. Construction drawing of the reproductive system of *Phagocata gracilis* showing the position of the various parts as viewed from the side, X 70.
- Fig. 33. Construction drawing of the reproductive system showing arrangement of the organs as viewed from above, X 70.
- Fig. 34. Cross section of the uterine duct showing general structure, X 100.
- Fig. 35. Cross section of one of the vasa deferentia in the region of the uterus, X 1000.
- Fig. 36. Cross section of an oviduct showing its structure and relation to the surrounding tissue cells, X 1000.

### PLATE 3

- Figs. 37-48. A complete series of 30mu. frontal sections through the uterus, sperm receptacle, and penis, showing all details of structure, X 50.
- Fig. 37. Section through the uppermost layers of the sperm receptacle.
- Figs. 38-39. Show uterus and uterine duct cut about midway, and the beginning of the anterior seminal chamber.
- Fig. 40. Shows beginning of muscular tube.
- Fig. 41. Section through sperm receptacle showing ventral wall of the disappearing uterus, the uterine duct becoming circular in form due to its turning downward, and the first appearance of the enlarged ends of the vasa deferentia within the sperm receptacle.
- Fig. 42. Similar to fig. 41, but showing in addition the posterior seminal chamber, and point of connection of the two oviducts.
- Fig. 43. Section cut slightly lower than fig. 42.
- Fig. 44. Typical frontal section through the sperm receptacle and penis.
- Fig. 45. Shows connection between walls of the main receptacle sheath and those of the penal sheath. Also the left vas deferens and its point of entrance into the sperm receptacle, and the common oviduct emptying into the muscular tube.



- Fig. 46. Section slightly lower than fig 45.
- Fig. 47. Section through the point of entrance of the uterine duct and muscular tube into the genital atrium; also entrance of right vas deferens into sperm receptacle.
- Fig. 48. Section through the genital atrium.
- Figs. 49-64. Series of transverse sections through the sperm receptacle and the organs associated with it, X 50.
- Fig. 49. Anterior end of receptacle showing its attachment to ventral wall of body.
- Fig. 50. Section through point of entrance of vasa deferentia.
- Figs. 51-52. Show relation of receptacle to sheath and uterine duct; also vasa deferentia and their corresponding internal ducts.
- Figs. 53-54. Sections showing muscular tube, anterior seminal chamber, and enlargement of vasa deferentia within the sperm receptacle.
- Figs. 55-56. Sections through the pinching off of muscular tube to form a complete duct; also union of the two vasa deferentia.
- Fig. 57. Section showing the anterior seminal chamber.
- Fig. 58. Section showing the connection between anterior and posterior seminal chambers, the looping back of the vasa deferentia, and the thickened wall of the uterine duct.
- Fig. 59. Section through the posterior seminal chamber; the oviducts have converged so as to lie near the median line of the body.
- Fig. 60. Section through the penis and the penal sheath.
- Fig. 61. Section showing last vestiges of sperm receptacle sheath.
- Fig. 62. Section showing union of oviducts.
- Fig. 63. Section showing connection of muscular tube and uterine duct with the genital atrium.
- Fig. 64. Section through point of entrance of the common oviduct into muscular tube.





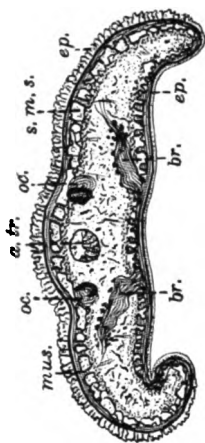


Fig. 4

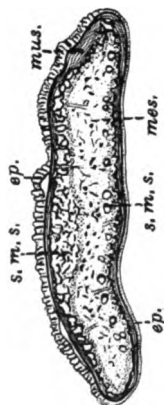


Fig. 3

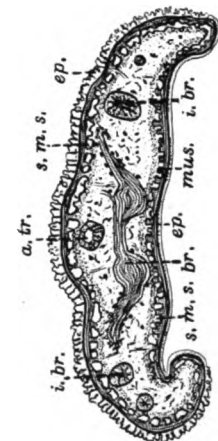


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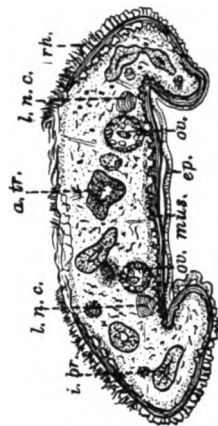


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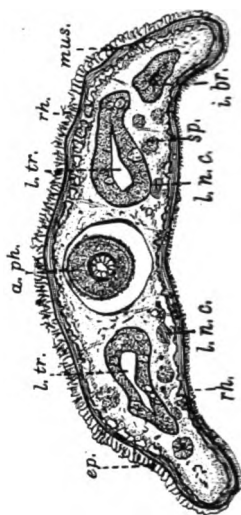


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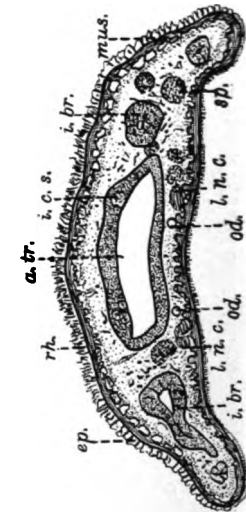


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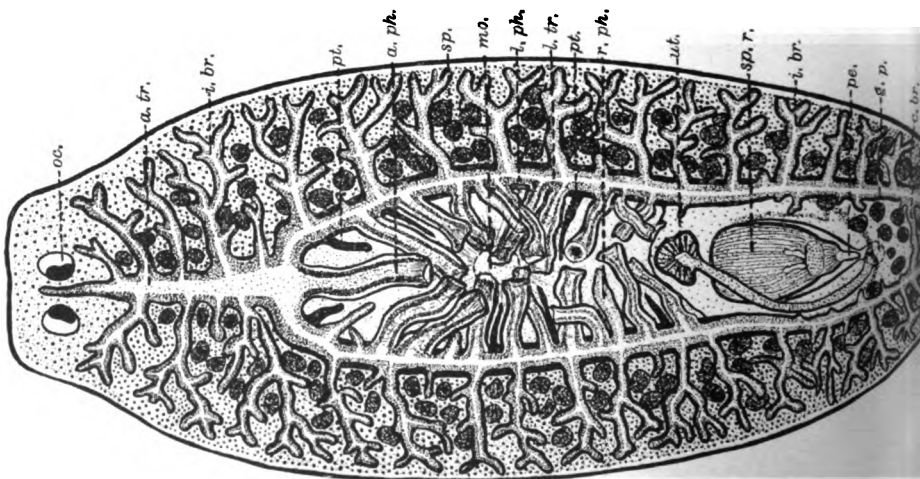


Fig. 2

pl. ph. mus. s. m. s.

s. m. s. ph. pl. s. m. s. l. tr. i. br. ep.

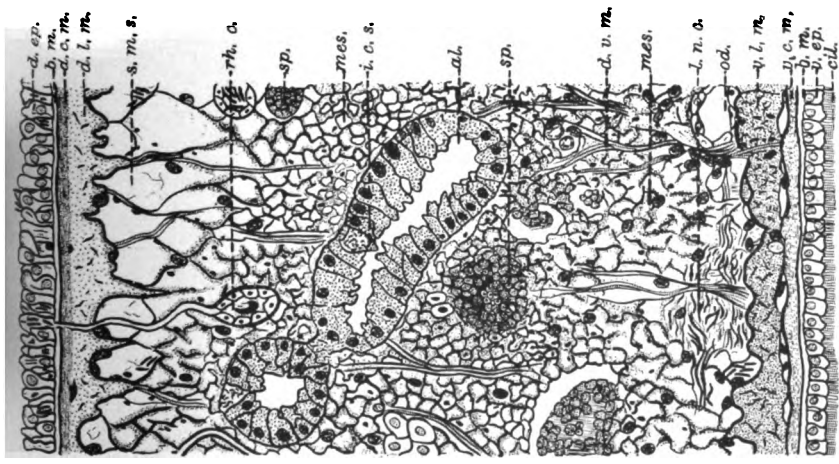


Fig. 2

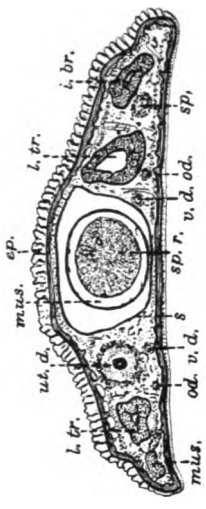


Fig. 12

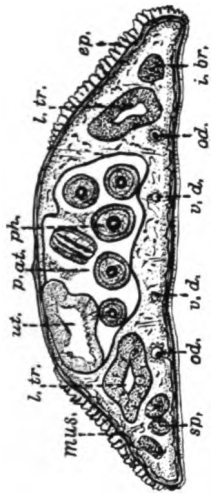


Fig. 11

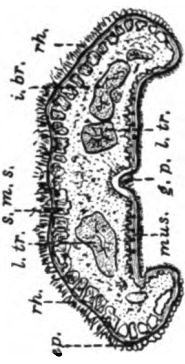


Fig. 14

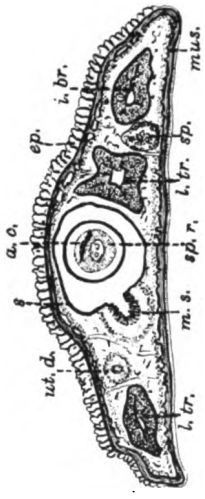


Fig. 13

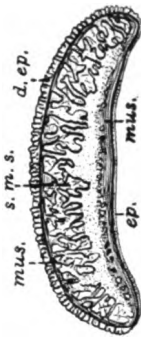


Fig. 16



Fig. 15

Plate I





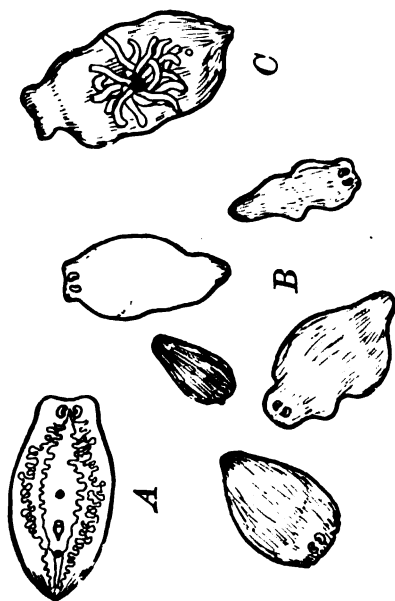


Fig. 17

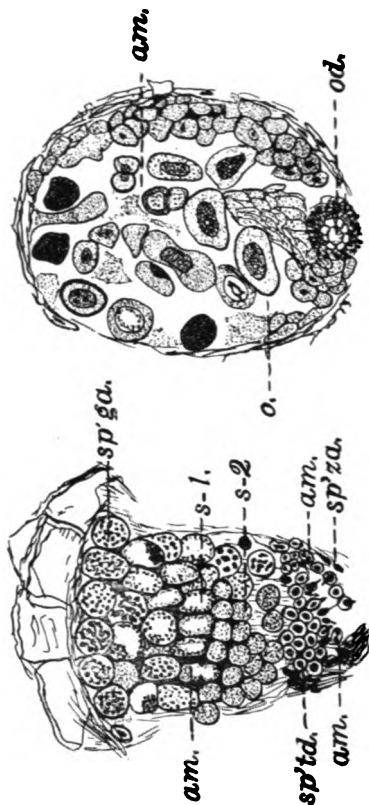


Fig. 18

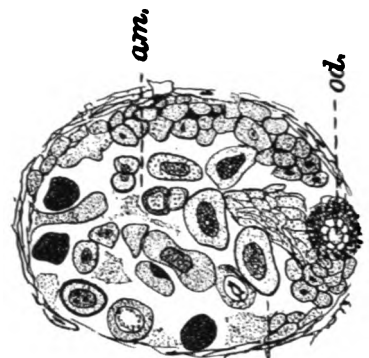


Fig. 19



Fig. 20



Fig. 21

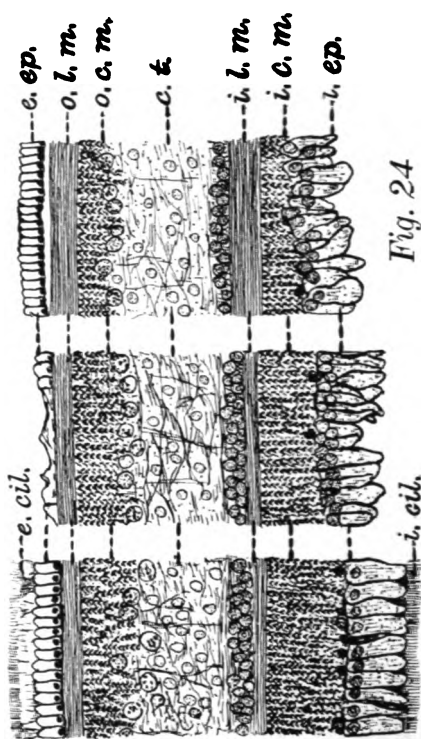


Fig. 24



Fig. 25

Fig. 23

Fig. 22

p. n.c. g. p.





Fig. 28



Fig. 27



Fig. 29



Fig. 30

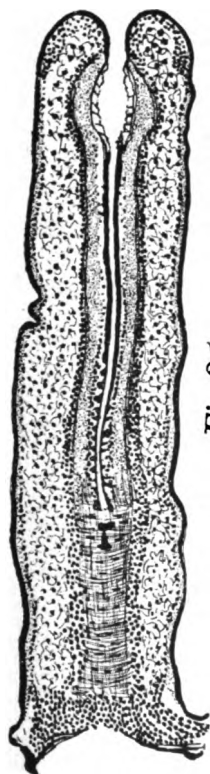


Fig. 31

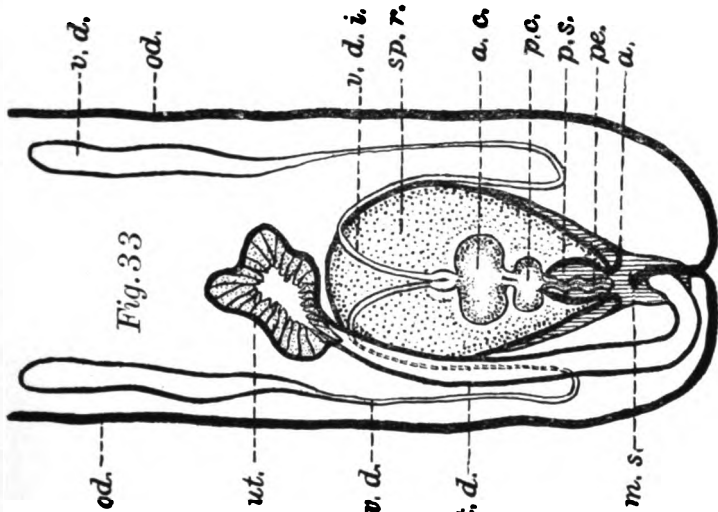


Fig. 33

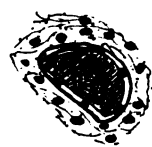


Fig. 34

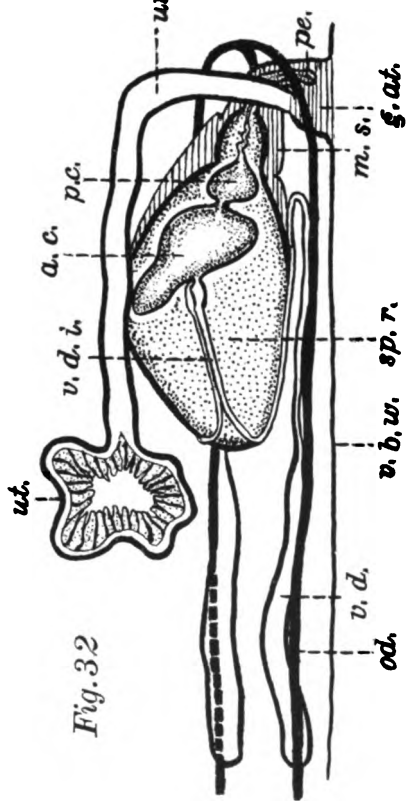


Fig. 32

Fig. 35

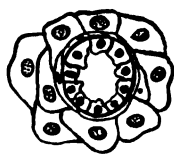


Fig. 36





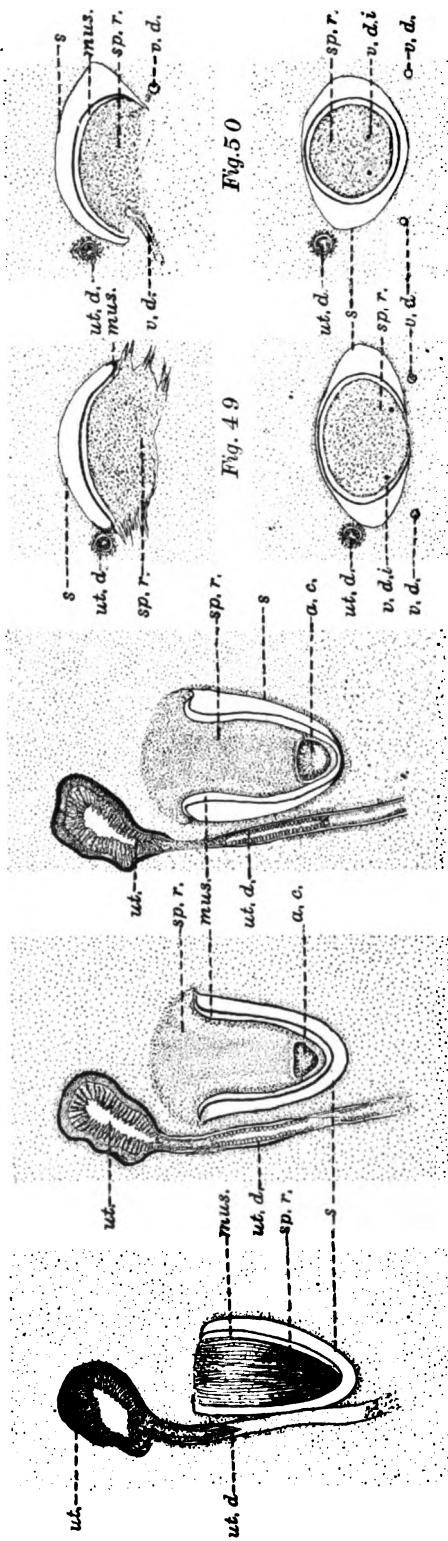


Fig. 37

Fig. 38

Fig. 39

Fig. 49

Fig. 50

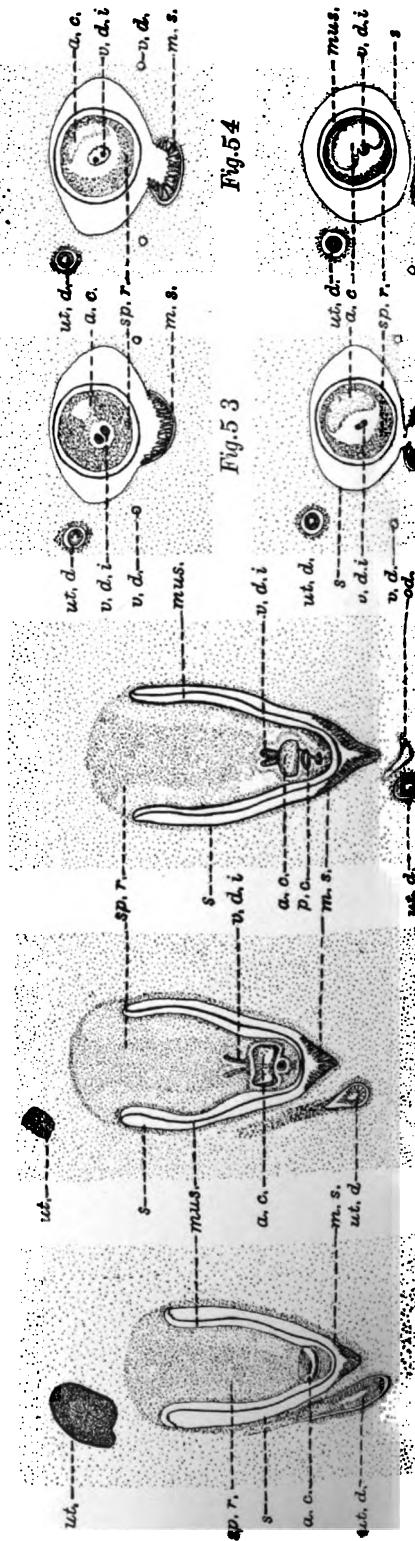


Fig. 51

Fig. 52

Fig. 53

Fig. 54

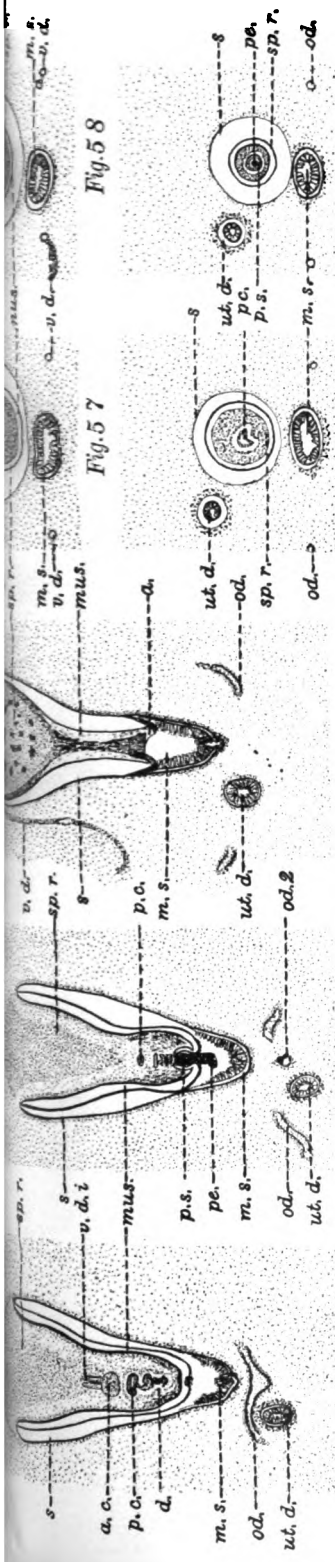


Fig. 43

Fig. 44

Fig. 45

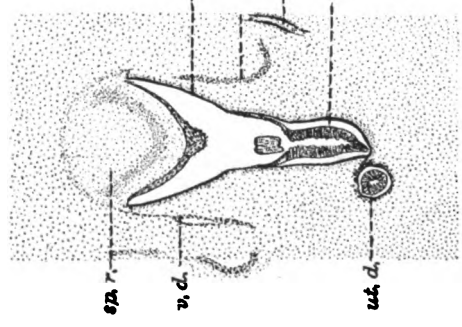


Fig. 46

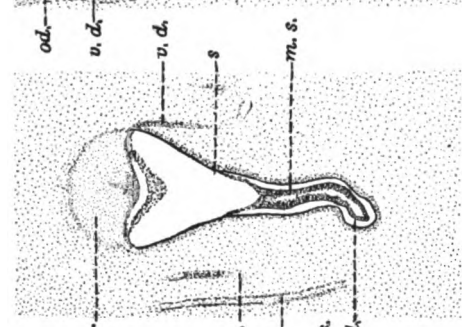


Fig. 47

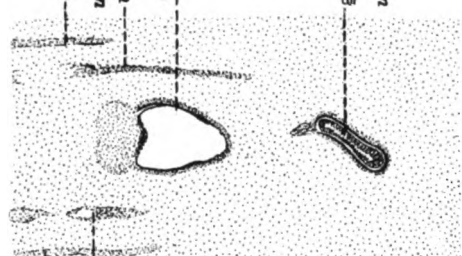


Fig. 48

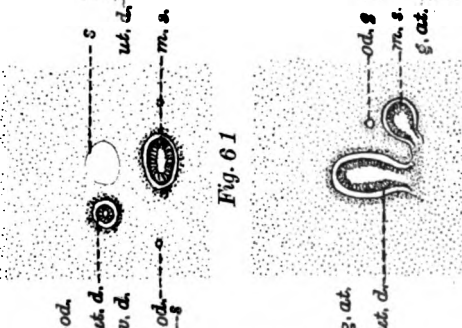


Fig. 59

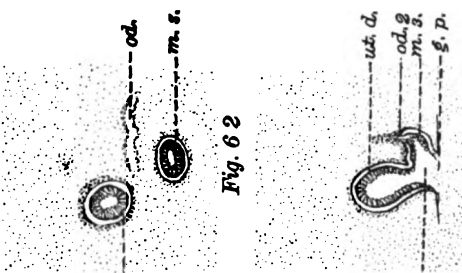


Fig. 60

Fig. 57

Fig. 58

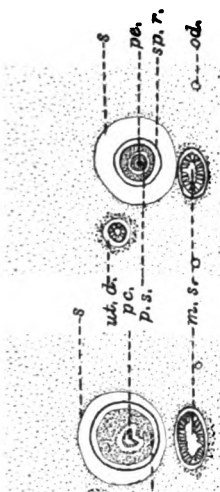


Fig. 61

Fig. 62



Fig. 63



Fig. 64

Plate III















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